QL
671
.W7
v.126
no.2

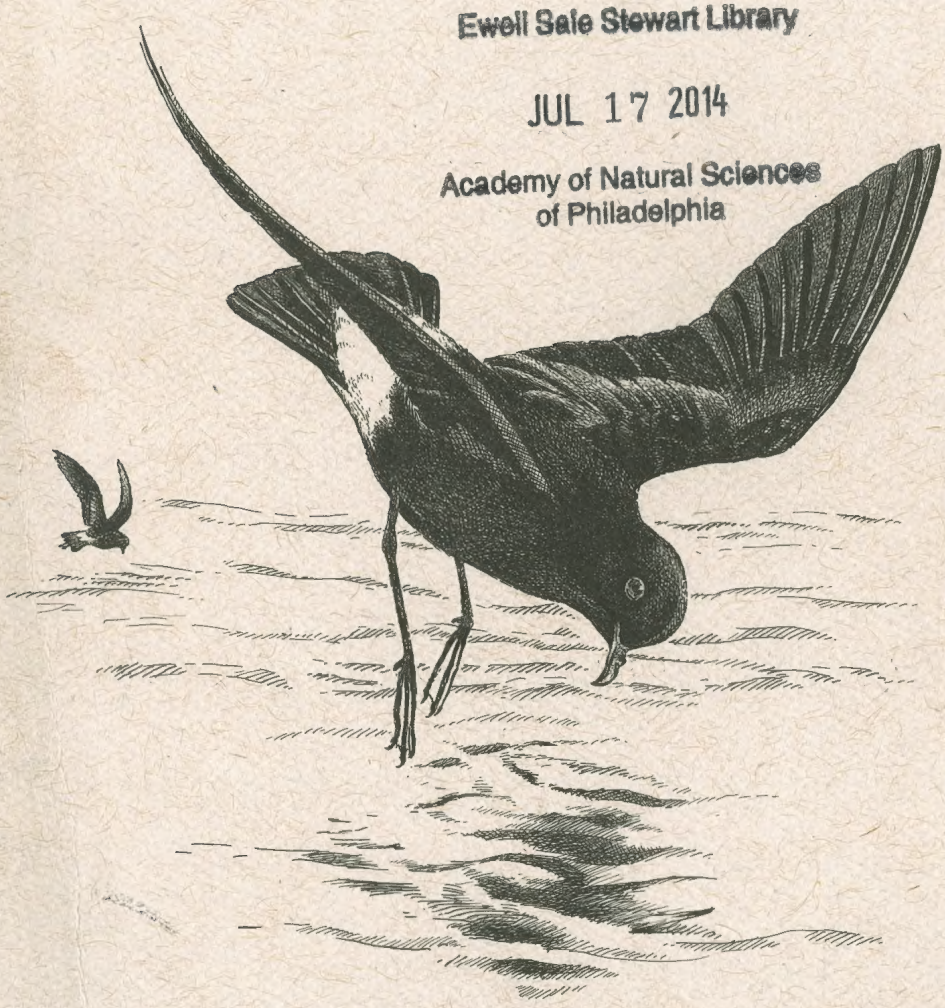
The Wilson Journal of Ornithology

Volume 126, Number 2, June 2014

Ewell Sale Stewart Library

JUL 17 2014

Academy of Natural Sciences
of Philadelphia



Published by the
Wilson Ornithological Society

QL671
W7
V. 126
NO. 2

THE WILSON ORNITHOLOGICAL SOCIETY
FOUNDED 3 DECEMBER 1888
Named after ALEXANDER WILSON, the first American ornithologist.

President—Robert L. Curry, Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA; e-mail: robert.curry@villanova.edu

First Vice-President—Sara R. Morris, Department of Biology, Canisius College, 2001 Main Street, Buffalo, NY 14208, USA, e-mail: morriss@canisius.edu

Second Vice-President—Mark E. Deutschlander, Department of Biology, Hobart & William Smith Colleges, 300 Pulteney Street, Geneva, NY 14456, USA; e-mail: deutschlande@hws.edu

Editor—Mary Bomberger Brown, School of Natural Resources, University of Nebraska, 3310 Holdrege Street, Lincoln, NE 68583-0995, USA, e-mail: wjo@unl.edu

Secretary—John A. Smallwood, Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwoodj@montclair.edu

Treasurer—Melinda M. Clark, 52684 Highland Drive, South Bend, IN 46635, USA; e-mail:wosclark@gmail.com

Elected Council Members—William H. Barnard, Margret I. Hatch, and Mark E. Hauber (terms expire 2014), Todd E. Katzner, Dennis G. Siegfried, and Lindsey Walters (term expire 2015), Kerri Cornell Duerr, Letitia Reichart, and Peter G. Saenger (terms expire 2016).

Living Past-Presidents—Douglas A. James, Jerome A. Jackson, Clait E. Braun, Richard C. Banks, Richard N. Conner, Keith L. Bildstein, Edward H. Burtt Jr., John C. Kricher, William E. Davis Jr., Charles R. Blem, Doris J. Watt, James D. Rising, E. Dale Kennedy, and Robert C. Beason.

Membership dues per calendar year are: Regular, $40.00; Student, $20.00; Family, $50.00; Sustaining, $100.00; Life memberships, $1,000.00 (payable in four installments).

The Wilson Journal of Ornithology is sent to all members not in arrears for dues.

THE WILSON JOURNAL OF ORNITHOLOGY
(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710, USA.

All articles and communications for publication should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, MI 48109, USA.

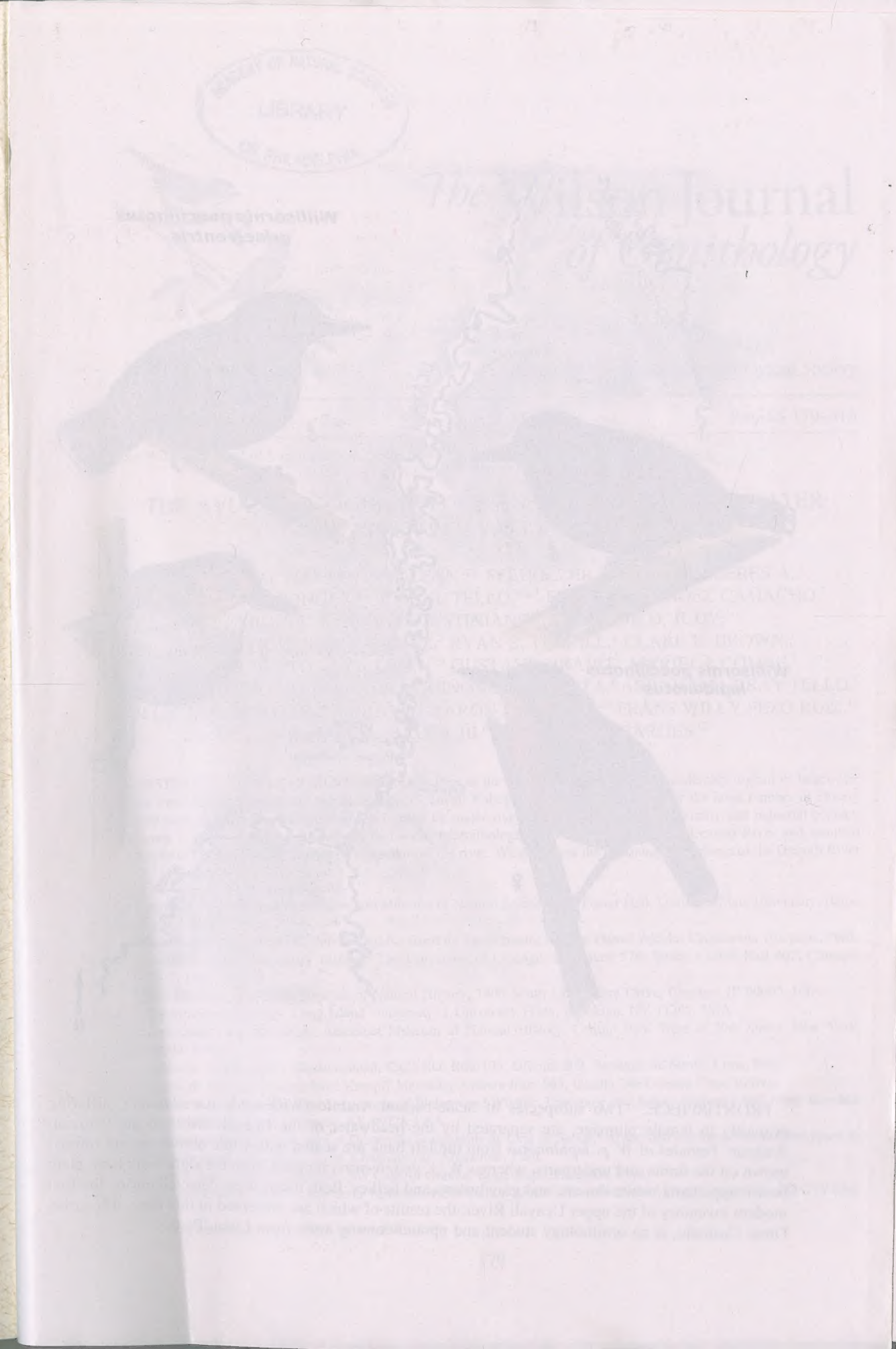
Subscriptions, changes of address, and claims for undelivered copies should be sent to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710, USA. Phone: (254) 399-9636; e-mail: business@osnabirds.org. Back issues or single copies are available for $12.00 each. Most back issues of the journal are available and may be ordered from OSNA. Special prices will be quoted for quantity orders. All issues of the journal published before 2000 are accessible on a free web site at the University of New Mexico library (http://elibrary.unm.edu/sora/). The site is fully searchable, and full-text reproductions of all papers (including illustrations) are available as either PDF or DjVu files.

© Copyright 2014 by the Wilson Ornithological Society
Printed by Allen Press Inc., Lawrence, KS 66044, USA.

COVER: Wilson's Storm-Petrel (*Oceanites oceanicus*). Illustration by Don Radovich.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

LIBRARY



FRONTISPIECE. Two subspecies of Scale-backed Antbird (*Willisornis poecilinotus*), differing primarily in female plumage, are separated by the headwater of the Ucayali River in the Peruvian Amazon. Females of *W. p. lepidonotus* from the left bank are scaled with white above and are rufous-brown on the throat and underparts, whereas *W. p. griseiventris* females from the right bank have plain brown upperparts, white throats, and gray breasts and bellies. Both forms were detected during the first modern inventory of the upper Ucayali River, the results of which are presented in this issue. The artist, Omar Custodio, is an ornithology student and up-and-coming artist from Lima, Peru.

ACADEMY OF NATURAL SCIENCES
LIBRARY
OF PHILADELPHIA

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 126, NO. 2 June 2014 PAGES 179–416

The Wilson Journal of Ornithology 126(2):179–191, 2014

THE AVIAN BIOGEOGRAPHY OF AN AMAZONIAN HEADWATER: THE UPPER UCAYALI RIVER, PERU

MICHAEL G. HARVEY,[1,13] GLENN F. SEEHOLZER,[1] DANIEL CÁCERES A.,[2] BENJAMIN M. WINGER,[3,4] JOSE G. TELLO,[5,6,7] FLOR HERNÁNDEZ CAMACHO,[7] MIGUEL A. APONTE JUSTINIANO,[8] CAROLINE D. JUDY,[1] SHEILA FIGUEROA RAMÍREZ,[7] RYAN S. TERRILL,[1] CLARE E. BROWN,[1] LUIS ALBERTO ALZA LEÓN,[7,9] GUSTAVO BRAVO,[1] MARIELA COMBE,[7] OMAR CUSTODIO,[7] ALESSANDRA QUIÑONEZ ZUMAETA,[7] ABRAHAM URBAY TELLO,[7] WILLY ANTONIO GARCIA BRAVO,[7] AARON Z. SAVIT,[3,4,10] FRANS WILLY PEZO RUIZ,[11] WILLIAM M. MAUCK III,[6] AND OLIVIER BARDEN[12]

ABSTRACT.—The Ucayali River is a major tributary of the Amazon, but it narrows considerably toward its headwater at the base of the Andes. This region, the upper Ucayali Valley, is of biological interest for the large number of closely related birds elsewhere separated from each other by major rivers that come into close proximity and potential contact. Between 2006–2011, we conducted the first modern ornithological inventory of the upper Ucayali River and sampled localities in all major avian habitats on either side of the river. We document the continued importance of the Ucayali River

[1] Department of Biological Sciences and Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA.

[2] Museo de Historia Natural, Universidad Nacional de San Agustín, Avenue Daniel Alcides Carrión s/n, Arequipa, Peru.

[3] Committee on Evolutionary Biology, The University of Chicago, 1025 East 57th Street, Culver Hall 402, Chicago, IL 60637, USA.

[4] Bird Division, The Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA.

[5] Department of Biology, Long Island University, 1 University Plaza, Brooklyn, NY 11201, USA.

[6] Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA.

[7] Centro de Ornitología y Biodiversidad, Calle Sta. Rita 105, Oficina 202, Santiago de Surco, Lima, Peru.

[8] Museo de Historia Natural Noel Kempff Mercado, Avenue Irala 565, Casilla 2489, Santa Cruz, Bolivia.

[9] Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska - Fairbanks, 982 North Koyukuk Drive, 101 Murie Building, Fairbanks, AK 99775, USA.

[10] Instituto de Investigación para el Desarrollo Sustentable de Ceja de Selva. Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas, Higos Urco, Chachapoyas, Amazonas, Peru.

[11] Avenue Jose Carlos Mariátegui, 368 Castillo Grande, Rupa Rupa, Huanuco, Peru.

[12] Centre d'étude de la forêt, Rue de la Terrasse 2405, Pavillon Abitibi-Price, Université Laval, Sainte-Foy, PQ G1V 0A6, Canada.

[13] Corresponding author; e-mail: mharve9@lsu.edu

as a biogeographic barrier, even at the headwater, but also find that some mixing occurs, both in the form of taxa crossing to the "wrong" bank and in the potential intergradation of distinct forms. We describe the biogeography of birds in the region, characterize the avifaunas of major habitats, and discuss in detail species of particular biogeographical interest. *Received 25 August 2013. Accepted 10 January 2014.*

Key words: Amazonia, biogeography, range extension, river barrier, river island, Ucayali, white sand.

The rivers of the Amazon Basin are important barriers to the distributions of terrestrial animals (Wallace 1852), even for relatively vagile taxa such as birds (Sick 1967, Haffer 1969). The narrowing of rivers in their headwaters regions, however, may result in the mixing of faunas and potential contact between otherwise geographically separated forms (Wallace 1852, Haffer 1992, Bates et al. 2004, Naka et al. 2012). The Ucayali River is a major headwater tributary of the Amazon River, but narrows to roughly 0.5 km in width in its uppermost reaches at the base of the Andes Mountains. The upper Ucayali River lies near the intersection of the Napo and Inambari areas of endemism (Cracraft 1985) and in an area with many distributional limits (Schulenberg et al. 2010). Therefore, it is a potential zone of contact between divergent populations or species separated downstream by the greater breadths of the lower Ucayali and Amazon rivers.

Avian distributional limits along the upper Ucayali River are unclear, because little ornithological work has been conducted in the region. Most information on the regional avifauna comes from the collections of Alfonso and Ramón Olalla, who worked on the uppermost Ucayali River for Frank M. Chapman and the American Museum of Natural History (AMNH) during 1927–1928. Accusations that the Olallas falsified specimen data arose in the 1960s, but a recent analysis suggests that much of their locality information is reliable and that their collections should be useful for biogeographical studies (Wiley 2010). No other work has been conducted on the upper Ucayali River since the 1920s, although expeditions have been made nearby to the Pucallpa area and Sierra del Divisor to the north (O'Neill and Pearson 1974, O'Neill et al. 1991, Whitney et al. 2004, Schulenberg et al. 2006a, Srinivas and Molina Vilca 2013), the Pachitea Valley and highlands of the Sira Mountains to the west (Weske 1972, Terborgh and Weske 1975, González M. 1998, Harvey et al. 2011, Socolar et al. 2012), the Urubamba River and slopes of the Vilcabamba Mountains to the south (Schulenberg 2001; M. J. Miller unpubl. data), and Balta in the Purus drainage well to the east (O'Neill 1969).

We present the results of the first modern ornithological surveys of the region surrounding the upper Ucayali River, including sites on both banks. We examine the influence of the upper Ucayali River on bird distributions and compare distributional patterns from this area to patterns based on prior fieldwork downriver along the middle Ucayali. We describe the bird communities of major habitats, and provide details on species of particular biogeographical interest. We compare our results to the Olalla collections and discuss the validity of their data and comment on the conservation importance of the region. We include a species list annotated with information on distribution, abundance, habitat, and status in the online Supplemental Material.

METHODS

Study Region

The upper Ucayali River forms at the confluence of the Tambo and Urubamba rivers and then flows northward along the eastern base of the Cerros del Sira (Fig. 1). The upper Ucayali River sits in a broad valley bounded to the west by the Cerros del Sira and to the east by hilly terrain extending to the upper Juruá River near the Brazil border. The valley of the upper Ucayali River comprises much of the western portion of the Region (formerly Department) of Ucayali. The climate is wet and hot, with mean annual rainfall of 2,950 mm and a mean annual temperature of 25 °C at Atalaya near the confluence of the Tambo, Urubamba, and Ucayali rivers (Oficina Nacional de Evaluación de Recursos Naturales 1968). The valley contains a diverse array of lowland Amazonian and Andean foothill habitats, several of which are important for ecologically specialized bird species. *Terra firme* forest is extensive in upland areas, and *várzea*-like floodplain forest is widespread on the alluvial plain of the whitewater Ucayali River and major tributaries. *Igapó*-like floodplain forest is localized around blackwater streams and *cochas*, or oxbow lakes. Stunted forest on sandy soil that resembles white sand forest (*varillal*) is very restricted in the region but occurs in a few small patches to the east of the alluvial plain of the Ucayali River.

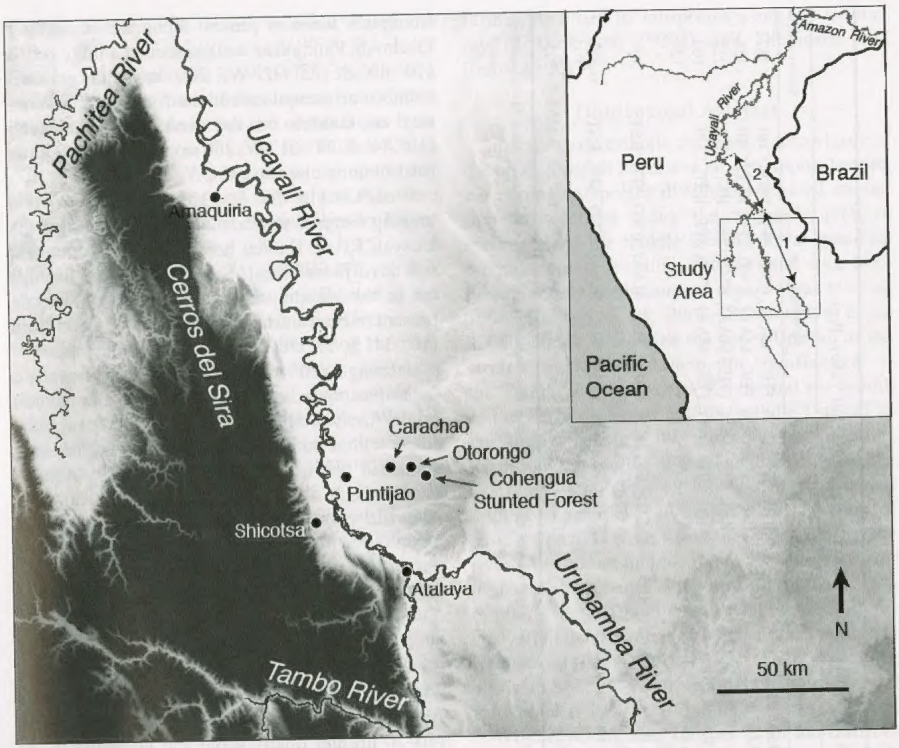


FIG. 1. A map of the study area showing the locations of primary study sites mentioned in the text. Numbers in the inset refer to sections of the Ucayali River used in the biogeographic analyses: (1) upper Ucayali River and (2) middle Ucayali River.

Lowland *Guadua* spp. bamboo occurs in small stands along the base of the Sira and may also occur in very large stands in the uplands well to the east of the Ucayali River. Palm swamps of *Mauritia* spp. occur in poorly drained locations throughout the area, including within the stunted forest. River edges and islands harbor a suite of successional habitats, and successional habitats also occur around the edges of the town of Atalaya and various indigenous communities. Along the eastern base of the Sira, the forest transitions gradually into lower montane evergreen forest between ~500–900 m.

Study Sites

The authors surveyed the region of the upper Ucayali River on a total of 160 days during six visits between 2006–2011 (Table 1). Inventory sites are scattered across the valley on both sides of the river (Fig. 1).

The Ucayali River is a meandering whitewater river that contains numerous islands and sandbars. River level fluctuates widely with season, and fallen trees and debris as well as the predominance of secondary habitat are evidence of fluvial effects on the landscape. For our purposes, this site contains all areas in and immediately adjacent to the river, including islands. Sampling effort was scattered along the river, although we made an effort to intensively sample an island in the mouth of the Tambo River (10° 71′ S, 73° 76′ W; 210 m). Habitats on this island were typical of other younger islands in the area and included sandy flats, *Gynerium* spp. cane, *Tessaria* spp. scrub, and *Cecropia* spp.-dominated woodland.

Puntijao (10° 41′ S, 73° 95′ W; 200 m) is a camp alongside the Quebrada Puntijao in the alluvial plain of the Ucayali River 7 km to the east of the river itself. Habitat here is primarily *várzea*-like floodplain forest, although *igapó*-like

TABLE 1. Sampling effort between 2006–2011 at study sites in the upper Ucayali Valley, Peru.

Site	Institutions	Habitats surveyed[a]	Dates surveyed	Surveyors	Species detected
Puntijao	CORBIDI, LSUMNS	V, C, W, R	19–25 June 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	237
Carachao	CORBIDI, LSUMNS	T, C	24–29 May 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	185
Otorongo	CORBIDI, LSUMNS	T, M	30 May–18 June 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	222
Cohengua Stunted Forest	CORBIDI, LSUMNS	S, T, M	2, 10–14 June 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	100
Ucayali River	CORBIDI, LSUMNS	R, I	Various dates in 2006, 2008, 2010, and 2011	All authors	139
Atalaya vicinity	CORBIDI, LSUMNS	T, V, C, R, W	Various dates in 2006, 2008, 2010, and 2011	MGH, GFS, DCA, BMW, FHC, MAAJ, CVD, SFR, RST, CEB, LAAL, GB, MC, OC, OB	306
Shicotsa	CORBIDI, LSUMNS	T, V, B, C, R	Various dates in 2008 and 2011	MGH, GFS, DCA, BMW, FHC, MAAJ, CVD, SFR, RST, GB, OC	248
Amaquiria	CORBIDI, AMNH	T, C, V, R	11–31 August 2009	JGT, SFR, LAAL, AQZ, AUT, WAGB, AZS, FWPR, WMM	295

[a] T = humid upland forest (*terra firme*), V = humid bottomland forest (*várzea* and *igapó*), S = stunted forest, C = clearings and successional areas, I = river islands, R = river and river edge, B = *Guadua* spp. bamboo, M = *Mauritia* spp. palm swamps, W = wetlands, O = overhead.

floodplain forest is present along the blackwater Quebrada Puntijao as well as around a large *cocha* (10° 40′ S, 73° 97′ W; 200 m). Successional habitats are present around the Ashéninka community of Galilea on the bank of the Ucayali (10° 44′ S, 74° 01′ W; 200 m) and along a logging road running close to camp.

Carachao (10° 38′ S, 73° 80′ W; 280 m) is a logging camp in uplands 24 km to the east of the Ucayali River. Habitat here is selectively logged, tall *terra firme* forest. Several *Mauritia* swamps are in the vicinity, and successional habitats are present in clear-cuts near the village of Chorinashi (10° 34′ S, 73° 78′ W; 270 m) to the north.

Otorongo (10° 38′ S, 73° 73′ W; 350 m) is a logging camp located in uplands 32 km to the east of the Ucayali River. Habitat is tall *terra firme* forest with a more open canopy than the forest at Carachao because of selective logging. A blackwater stream, Quebrada Yanayacu, lined with *Mauritia* palms, is located 2 km to the east of camp (10° 38′ S, 73° 71′ W; 340 m). Forest to the east of camp transitions gradually to stunted forest.

The Cohengua Stunted Forest (10° 41′ S, 73° 68′ W; 370 m) is an area of scrub and short-stature forest on poorly drained, sandy soil 36 km east of the Ucayali River. A gradual transition occurs from tall (30+ m) *terra firme* forest in the vicinity of Otorongo to shorter forest (10–20 m) and finally scrub and grassland in the center of the Cohengua Stunted Forest. Low-lying areas are often flooded and are dominated by grasses and *Mauritia* palms. Small blackwater streams are located throughout.

Atalaya (10° 73′ S, 73° 75′ W; 220 m), the only town in the upper Ucayali Valley, is on the Tambo River just above its confluence with the Urubamba River. Pastures and scrub surround the town and patches of *terra firme* and *várzea*-like floodplain forest occur on the outskirts. Ridges west of town contain forest that transitions to lower montane evergreen forest. Survey effort was concentrated around Atalaya itself as well as at Canuja (10° 79′ S, 73° 77′ W; 240–450 m), an Ashéninka community and hydroelectric facility located just over the border into Junín Region 6 km south of Atalaya.

Shicotsa (10° 44′ S, 74° 10′ W; 320 m) is a camp along the Quebrada Shicotsa near the Ashéninka community of Pensylvania. The camp is at the base of the Cerros del Sira 8 km west of the Ucayali River. Habitat here is dominated by tall *terra firme* forest on hilly terrain, with a

gradual transition to lower montane evergreen forest with increasing elevation. A patch of *Guadua* spp. bamboo is located along the top of a small ridge at the base of the slopes of the Cerros del Sira. We include in this site observations from nearby areas between Shicotsa and Misíon Unine (10° 64′ S, 73° 97′ W; 250 m) to the south that were of similar habitat and terrain and that were sampled opportunistically during visits to higher elevations.

Amaquiria (9° 46′ S, 74° 38′ W; 170 m) is a Shipibo-Conibo native community located at the west bank of the Tipishca Amaquiria River in the Reserva Comunal El Sira. Habitat along the river margins here includes successional vegetation dominated by *Tessaria* spp. and river and forest edge vegetation bordering the community. We also treat as part of this site, two other camps in the same area: Sipiria (9° 47′ S, 74° 44′ W; 173 m) on the west side of Quebrada Sipiria at Puesto de Vigilancia No.1 in the Reserva Comunal El Sira, with habitats dominated by tall *terra firme* forest, *várzea*-like forest, and some clearings and successional habitats; and Tambo (9° 47′ S, 74° 48′ W; 250–500 m), on the west side of Quebrada Tambo in the Reserva Comunal El Sira at the base of the Cerros del Sira with tall terra firme forest transitioning rapidly to lower montane evergreen forest with increasing elevation.

Fieldwork

We conducted observational surveys along transects that followed logging tracks, trails, or water courses between 0500–1200 PET and often again between 1400–1830. We tallied all birds seen or heard, recorded habitat associations, made audio recordings, and collected birds using shotguns and mist-nets. Observation data were deposited in the Avian Knowledge Network through the eBird portal, Cornell Laboratory of Ornithology, Ithaca, New York, USA. We archived audio recordings at the Macaulay Library (ML), Cornell Laboratory of Ornithology. Voucher specimens and tissue samples were deposited at the Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru; the Louisiana State University Museum of Natural Science (LSUMNS), Baton Rouge, Louisiana, USA; and the American Museum of Natural History (AMNH), New York, USA. Birds were identified to species using the taxonomy of the South American Classification Committee of the American Ornithologist's Union (Remsen et al. 2013). Where possible, birds were further identified to subspecies using the taxonomy of Dickinson (2003) and Dickinson and Remsen (2013).

Distributional Analyses

In order to investigate the relative importance of the upper Ucayali River as a biogeographic barrier, we compared species distributions based on our inventory results along the upper Ucayali to records along the middle Ucayali River based on compilations of existing distributional data from this relatively well-sampled region (Parker et al. 1996; Ridgely et al. 2003; Schulenberg et al. 2006b, 2010). We define the upper Ucayali as the stretch of river between the confluence of the Tambo and Urubamba Rivers and the mouth of the Pachitea River, and the middle Ucayali as the stretch between the mouth of the Pachitea River and the mouth of the Pauya River near the Cordillera Azul (Fig. 1). For both the upper and middle Ucayali, we generated a list of pairs of closely related species that are separated by the river. We did not include the lower Ucayali River in this analysis because the bird life in that region is poorly known, and because the course of the Ucayali in that region is known to have undergone frequent shifts (Dumont 1991) that may have allowed species pairs to mix (Tuomisto and Ruokolainen 1997).

We did not include subspecies in the distributional analysis of the upper and middle Ucayali River because the subspecific taxonomy of many Amazonian species is in need of revision (Remsen et al. 2013). We were interested in the role of the upper Ucayali River in structuring intraspecific diversity, however, and we examined our results from the upper Ucayali to determine which species contained multiple phenotypically diagnosable forms within the study area. If possible, we assigned these forms to subspecies based on the taxonomy of Dickinson (2003) and Dickinson and Remsen (2013). We stress that subspecies assignments should be considered preliminary and are used here as a convenience absent an alternative means of describing the observed intraspecific variation.

RESULTS

We recorded 564 bird species representing 66 families below 900 m elevation in the study region, 393 of which were documented with specimens or audio recordings. Species recorded above 900 m elevation during our surveys are

TABLE 2. Species pairs with distributions that are limited by either the upper or middle Ucayali River.

Genus	West bank species	East bank species	Limited by middle Ucayali?[a]	Limited by upper Ucayali?[b]	Species crossing river
Galbula	*albirostris*	*cyanicollis*	Yes	Yes	-
Malacoptila	*fusca*	*semicincta*	Yes	Yes	-
Nonnula	*brunnea*	*sclateri*	Yes	No	*sclateri*
Picumnus	*lafresnayi*	*aurifrons*	Yes	Yes	-
Pionites	*melanocephalus*	*leucogaster*	Yes	No	*leucogaster*
Frederickena	*fulva*	*unduliger*	Yes	Yes	-
Gymnopithys	*lunulatus*	*salvini*	Yes	No	*salvini*
Hemitriccus	*zosterops*	*griseipectus*	Yes	Unknown	-
Pheugopedius	*coraya*	*genibarbis*	Yes	No	see text

[a] Based on Parker et al. (1996), Ridgely et al. (2003), Schulenberg et al. (2006b), and Schulenberg et al. (2010).
[b] Based on results from this inventory.

discussed in Harvey et al. (2011). We recorded 455 species west of the Ucayali River, 382 species east of the Ucayali River, and 139 species on the river itself, including on river islands. Five hundred and three of the species observed are Amazonian residents, and the remainder are species distributed primarily in the Andes or vagrants from elsewhere. Twenty-one species of austral migrants and 21 species of boreal migrants were recorded. Of the Amazonian residents, 462 are present on both sides of the Amazon River, nine are species that are primarily northern Amazonian (north of the Amazon River) in distribution (based on Parker et al. 1996), and 32 are species that are primarily southern Amazonian. Additional information on distribution among the study sites, relative abundance, habitat, documentation, migratory status, and biogeographic affinities for each species and subspecies identified is in the online Supplemental Material.

Biogeography and the Ucayali River

We found the middle Ucayali River serves as a distributional break to nine species pairs (Table 2). In contrast, the upper Ucayali River within our study area delimits only four pairs, all of which are delimited by the middle Ucayali River. Sufficient distributional data from the upper Ucayali River are lacking for one pair that is delimited by the middle Ucayali. Of the four species pairs that are not delimited by the upper Ucayali River, in three the species typically found on the east bank also occurs on the west bank. In the fourth species pair not delimited by the upper Ucayali River, the details of the distribution of both species are unclear because of the presence of individuals with intermediate phenotypes.

Further scrutiny of variation within species revealed 11 species in which two diagnosable forms were present within the study area (Table 3). Eight of the 11 pairs of diagnosable forms appeared, based on our records, to be delimited by the Ucayali River. We observed phenotypic evidence of introgression in two subspecies pairs and one species pair that are sufficiently distinct phenotypically to recognize intermediates. Black-necked Stilt (*Himantopus mexicanus*) individuals present along the upper Ucayali River variously resembled either the black-backed *H. m. mexicanus* or white-backed *H. m. melanurus*, and some had apparent intermediate shades of gray on the back and hindneck. On the west side of the Ucayali River, Blue-crowned Manakin (*Lepidothrix coronata*) resembled the green-bodied form *L. c. exquisita*, distributed west of the Ucayali north to the Marañon. Individuals on the east side of the Ucayali River, however, were various shades of greenish-black and appeared to be intermediate between the black-bodied form *L. c. coronata* found east of the Ucayali River and a green-bodied form, either *L. c. exquisita* or *L. c. caelestipileata* of southeastern Peru. Members of the Coraya (*Pheugopedius coraya*) and Whiskered (*P. genibarbis*) Wren species pair along the upper Ucayali River are highly variable in plumage, but many appear intermediate between the two species.

Habitat Associations

Birds of Terra Firme Forest.—We recorded 324 bird species representing 45 families in *terra firme* forest on both sides of the river, and detected 155 species only in this habitat. Thamnophilidae (43 species) and Tyrannidae (42 species) were the most diverse families.

TABLE 3. Species within which we detected multiple diagnosable forms in the study area.

Genus/species	Hypothetical taxon 1	Hypothetical taxon 2	Hypothetical barrier
Himantopus mexicanus	*mexicanus*	*melanurus*	?[a]
Phaethornis malaris	*moorei*	*"ucayalii"*[b]	Ucayali River
Capito auratus	*punctatus*	*insperatus*	Ucayali River
Myrmoborus leucophrys	*koenigorum*[c]	*leucophrys*	?[a]
Willisornis poecilinotus	*lepidonotus*	*griseiventris*	Ucayali River
Dendrocincla fuliginosa	*phaeochroa*	*atrirostris*	Ucayali River
Dendrocolaptes certhia	*radiolatus*	*juruanus*	Somewhere on west bank of Ucayali River
Philydor erythrocercum	*lyra*	*ochrogaster*	Ucayali River
Lepidothrix coronata	*exquisita*	*coronata*[d]	Ucayali River
Schiffornis turdina	*steinbachi*	*amazona*	Ucayali River
Microcerculus marginatus[e]	*marginatus* (N voice type)	*marginatus* (S voice type)	Ucayali River

[a] Presence of intermediates complicates determination of a barrier.
[b] This taxon (Zimmer 1950) may represent intergrades between *P. m. moorei* and *P. m. bolivianus* (Hinkelmann 1996).
[c] *M. l. koenigorum* is described from the Huallaga Valley (O'Neill and Parker 1997), but individuals in the Sira resemble this form in plumage and are generally distinguishable from lowland populations.
[d] Individuals appear intermediate between *L. c. coronata* and a green-bodied form (presumably *L. c. exquisita* or *L. c. caelestipileata*).
[e] Although treated as the same subspecies, vocal differences between these populations are well known (e.g. Ridgely and Tudor 1989).

Birds of Floodplain Forest.—We recorded 237 bird species representing 40 families in *várzea*- and *igapó*-like floodplain forests, and detected 36 species only in these habitats. Thamnophilidae (30 species) and Tyrannidae (28 species) were the most diverse families. One-hundred and forty-six species were shared between *terra firme* and floodplain forest.

Birds of Successional Habitats.—We recorded 129 bird species representing 34 families in open and successional habitats. Tyrannidae (27 species) and Thraupidae (16 species) were the most diverse families. Many of the species recorded in this habitat are widespread in open areas in the Amazon Basin, but we also recorded some species that are rare and local in Amazonia, including Barn (*Tyto alba*) and Burrowing (*Athene cunicularia*) owls and Pearl Kite (*Gampsonyx swainsonii*). Migrants were numerous in this habitat; we recorded nine boreal and 15 austral migrant species, including rare migrants (Schulenberg et al. 2010) such as Slaty Elaenia (*Elaenia strepera*) and Plain Tyrannulet (*Inezia inornata*).

Birds of Stunted Forest.—We recorded 45 bird species representing 20 families in stunted forest, and detected eight species (and one subspecies) only in this habitat. Tyrannidae (nine species), Thamnophilidae (four species), and Furnariidae (four species) were the most diverse families. In the most stunted sections of forest (1–10 m canopy height), birds were scarce. Scissor-tailed Nightjar (*Hydropsalis torquata*), Rufous-throated Sapphire (*Hylocharis cyanus*), Zimmer's Tody-Tyrant (*Hemitriccus minimus*), one subspecies of Fuscous Flycatcher (*Cnemotriccus fuscatus duidae*), Brown-crested Flycatcher (*Myiarchus tyrannulus*), and Black Manakin (*Xenopipo atronitens*) were found only within this habitat. A few birds reached higher density in this habitat than elsewhere, including Scaled Pigeon (*Patagioenas fasciata*), White-flanked Antwren (*Myrmotherula axillaris*), Cinnamon Neopipo (*Neopipo cinnamomeus*), and Epaulet Oriole (*Icterus cayanensis*). Five presumed migrant species were recorded in the stunted forest, although it is possible some of these, such as *Hydropsalis torquata* and *Myiarchus tyrannulus*, breed locally. In forest of moderate canopy height fringing the stunted forest, Brazilian Tinamou (*Crypturellus strigulosus*), Brown-banded Puffbird (*Notharchus ordii*), Paradise Jacamar (*Galbula dea*), Bar-bellied Woodcreeper (*Hylexetastes stresemanni*), Lineated Woodcreeper (*Lepidocolaptes albolineatus*), Rufous-winged Foliage-Gleaner (*Philydor erythropterum*), Slender-billed Xenops (*Microxenops milleri*), Yellow-browed Antbird (*Hypocnemis hypoxantha*), Rufous-tailed Flatbill (*Ramphotrigon ruficauda*), Citron-bellied Attila (*Attila citriniventris*), Thrush-like Schiffornis (*Schiffornis turdinus*), Yellow-backed Tanager (*Hemithraupis flavicollis*), and Short-billed Honeycreeper (*Cyanerpes nitidus*) reached their highest local densities. Silky-tailed Nightjar (*Caprimulgus sericocaudatus*) was only recorded here. In isolated open palm swamps (*aguajales*) within the stunted forest, the two palm swamp specialists Point-tailed Palmcreeper (*Berlepschia rikeri*) and Sulphury Flycatcher

(*Tyrannopsis sulphurea*) were common, as were Smooth-billed Ani (*Crotophaga ani*), Swallow-winged Puffbird (*Chelidoptera tenebrosa*), and Palm Tanager (*Thraupis palmarum*), species typical of disturbed or riverine habitats and not generally found in *terra firme*.

Birds of Bamboo Patches.—We recorded 10 bird species representing five families in the bamboo, and detected six species only in this habitat. Thamnophilidae (three species) and Tyrannidae (three species) were the most diverse families. Birds known to specialize on bamboo (Kratter 1997) that we observed in this habitat were Rufous-breasted Piculet (*Picumnus rufiventris*), Dusky-cheeked Foliage-Gleaner (*Anabazenops dorsalis*), Red-billed Scythebill (*Campylorhamphus trochilirostris*), Dot-winged Antwren (*Microrhopias quixensis*), Striated Antbird (*Drymophila devillei*), Manu Antbird (*Cercomacra manu*), Large-headed Flatbill (*Ramphotrigon megacephalum*), Dusky-tailed Flatbill (*R. fuscicauda*), and White-cheeked Tody-Flycatcher (*Poecilotriccus albifacies*). We also observed the *obscurus* subspecies of Long-billed Gnatwren (*Ramphocaenus melanurus obscurus*) primarily in or adjacent to bamboo. In addition, the Olallas collected White-lined Antbird (*Percnostola lophotes*), a species often associated with bamboo (Kratter 1997), in the region in 1928 (Appendix II).

Birds of River Islands.—We recorded 37 bird species representing 12 families on islands in the Ucayali and lower Tambo rivers, and detected 13 species (and one subspecies) only in this habitat. Tyrannidae (11 species) and Thraupidae (six species) were the most diverse families. Species restricted to this habitat in the region, many of which have been classified as river island specialists (Rosenberg 1990), included Black-banded Crake (*Anurolimnas fasciatus*), Festive Parrot (*Amazona festiva*), Lesser Hornero (*Furnarius minor*), White-bellied (*Synallaxis propinqua*) and Parker's (*Cranioleuca vulpecula*) spinetails, Castelnau's Antshrike (*Thamnophilus cryptoleucus*), Black-and-white Antbird (*Myrmochanes hypoleucus*), Spotted Tody-Flycatcher (*Todirostrum maculatum*), River Tyrannulet (*Serpophaga hypoleuca*), Lesser Wagtail-Tyrant (*Stigmatura napensis*), Spotted Tody-Flycatcher (*Todirostrum maculatum*), one subspecies of Fuscous Flycatcher (*Cnemotriccus fuscatus fuscatior*), and Riverside Tyrant (*Knipolegus orenocensis*). Olive-spotted Hummingbird (*Leucippus chlorocercus*) was most common on river islands, but was also observed once in successional habitat near Atalaya, and several times in flight between islands and the shoreline.

Range Extensions and Vagrants

We recorded 22 species well outside of their known ranges (Schulenberg et al. 2006b, 2010). These records represent either range extensions for species that are likely resident in the region, or records of presumed wandering individuals from elsewhere. Below, we provide brief accounts for these species and biogeographic context based on a review of prior records:

Black-bellied Whistling-Duck (Dendrocygna autumnalis).—A single individual was observed at Otorongo by MGH flying overhead at dawn on 7 June 2011, and three individuals were observed by GFS and RST flying low over Atalaya at dusk on 7 July 2011. This species is rare in Peru, and primarily known from the Pacaya-Samiria region to the north. These are the first records from Ucayali Region.

Brazilian Teal (Amazonetta brasiliensis).—A pair was observed by MGH at close range on 7 May 2011 on the river island at the mouth of the Tambo River. They were not relocated on subsequent visits to the site. This species is presumably a very rare austral migrant to Peru, with few prior records, all from Madre de Dios Region. It appears to have become increasingly common, however, in recent years (MGH, pers. obs.; T. Schulenberg pers. comm.).

Puna Ibis (Plegadis ridgwayi).—DCA, MGH, SFR, and FHC observed a flock of four individuals flying over an open field bordering Quebrada Yanayacu along the track between Carachao and Chorinashi (10° 35′ S, 73° 78′ W; 290 m). The birds circled low overhead before flying southeast. This species is restricted to high altitude wetlands in the Andes and is a rare vagrant to the western Amazon Basin. This is the first record for Ucayali Region.

Black-faced Hawk (Leucopternis melanops).—An individual was observed on 6 January 2008 at the edge of a pasture outside of Atalaya (BMW, GFS, MGH). *L. melanops* is typically a species of northern Amazonia, where it was thought to replace the similar White-browed Hawk (*L. kuhli*), but it has recently been detected in a number of localities in the southwestern and south-central Amazon (Barlow et al. 2002, Raposo do Amaral et al. 2007, Shrum et al.

2011). In many of these locations, including in our study area, *L. melanops* and *L. kuhli* appear to be present in sympatry. This is the first record of *L. melanops* from Ucayali Region.

Burrowing Owl (Athene cunicularia).—Burrowing Owls were observed on at least three occasions in fields around the town of Atalaya and on river islands in the Tambo River and Ucayali River. Two agitated adults and two downy young barely capable of flight were observed on 17 October 2008 in a field southeast of Atalaya (MGH). Two adults, including a female with a calcified egg in the oviduct, were collected on an island in the Tambo River on 24 July 2010 (LAAL, GB, MGH, FHC). Formerly unknown from the Peruvian Amazon, this species has recently been found in small numbers in agricultural areas and along rivers in Loreto and Madre de Dios Regions. These records constitute the first for Ucayali Region and the first documented breeding observations from the Peruvian Amazon.

Fiery Topaz (Topaza pyra).—This species was first detected in the study area at Canuja 20–22 July 2010. At least three males and one female were observed feeding and interacting over a rocky stream in foothills at 450 m, and two males were collected. At least two males were observed and one male was collected at Carachao 24–29 May 2011. Here, they occurred in *aguajales* within terra firme forest. *Topaza pyra* was previously known in Peru only from Loreto Region in the northeast. The closest prior record, and the previous southernmost record for the species, comes from the Sierra del Divisor 350 km to the north (Schulenberg et al. 2006a).

Rufous-throated Sapphire (Hylocharis sapphirina).—One individual was netted and collected at the Cohengua Stunted Forest on 12 June 2011. This is the first record of this species from south of the Amazon River and east of the Ucayali River in Peru.

Brown-banded Puffbird (Notharchus ordii).—This species was fairly common at Otorongo and in the Cohengua Stunted Forest 2–13 June 2011. It occurred chiefly in taller stunted forest, but was present in tall *terra firme* forest as well. We obtained audio recordings and four specimens. This species is patchily distributed in Peru, often in areas with nutrient poor soils. This is the first record from Ucayali, with the closest prior record in the Sierra del Divisor 350 km to the north (Schulenberg et al. 2006a). These records bridge a gap in the distribution of *N. ordii* between the *varillales* of Loreto Region and a few isolated records in Madre de Dios Region.

Spotted Puffbird (Bucco tamatia).—Two individuals (a male and female) were netted and collected in *terra firme* forest at Otorongo on 2 June 2011. This species was previously known in Peru only from Loreto Region and an isolated record in Madre de Dios Region. This is the first record from Ucayali Region.

Short-billed Leaftosser (Sclerurus rufigularis).—Two individuals were collected in *terra firme* forest at Otorongo on 6 and 10 June 2011. This species was previously known in Peru only from Loreto Region. These constitute the first records for Ucayali Region and a range extension of 300 km to the south.

Fulvous Antshrike (Frederickena fulva).—A single male was observed and recorded by JGT on 27 August 2009 in dense understory of *terra firme* forest at ~300 m at Tambo on the west side of the Ucayali River. The recorded loudsong of this individual was consistent with *F. fulva* and distinct from the Undulated Antshrike (*F. unduliger*) recorded by GFS at Otorongo on the east side of the Ucayali River. This record extends the distribution of *F. fulva* 290 km south-southeast from the Rio Cushabatay, Loreto Region (Isler et al. 2009).

Black Bushbird (Neoctantes niger).—This species was uncommon in edge habitats at Carachao and Otorongo 27 May–15 June 2011. We obtained audio recordings and four specimens, including one female specimen with associated recordings. This is the first record from Ucayali Region and bridges a gap in the distribution of *N. niger* between Loreto and Madre de Dios Regions.

Zimmer's Tody-Tyrant (Hemitriccus minimus).—This species was fairly common in stunted forest of 8–15 m canopy height in the Cohengua Stunted Forest. We obtained audio recordings of songs and calls of several individuals. These are the first records for Ucayali Region and represent a range extension of 400 km from the nearest localities in Loreto Region.

Yellow-throated Spadebill (Platyrinchus flavigularis).—A single individual was observed and recorded by JGT on 28 August 2009 on a ridge at ~450 m near Tambo. The vegetation in this area is transitional between *terra firme* forest and montane evergreen forest. This species is known from few localities on the east slope of the Peruvian Andes and outlying ridges from 1,200–2,000 m (Schulenberg et al. 2006b, 2010), but this record constitutes the first record for Ucayali Region, the

first record for the Sira Range, and a downward elevational range extension of ~750 m.

Cinnamon Neopipo (Neopipo cinnamomea).—This species was first detected in the study area when one was netted and collected in foothill forest at 300 m at Canuja on 20 July 2010. Between 30 May–14 June 2011, we found it to be rare in *terra firme* forest at Otorongo and fairly common at the Cohengua Stunted Forest, where one individual was recorded and collected. This species is local in much of its range. The closest generally accepted records are from Huánuco and Madre de Dios Regions, although the Olallas collected a specimen from Santa Rosa (near Atalaya) in 1927.

Fuscous Flycatcher (Cnemotriccus fuscatus).—At least two subspecies were recorded in the region. *Cnemotriccus f. fuscatior* was commonly recorded on river islands in the Ucayali and Tambo rivers 16–19 October 2008, 24 July 2010, and 7 May–2 July 2011. We obtained eight specimens of this subspecies. *C. f. duidae* was fairly common at the Stunted Forest 11–14 June 2011, and we obtained audio recordings and five specimens. These are the first records of *C. f. duidae* from Ucayali Region. The nearest previous records are from the Sierra del Divisor in southern Loreto Region (Schulenberg et al. 2006a). These two taxa are widely sympatric (here within 36 km of each other), occur in different habitats, and have different vocalizations, and thus should be treated as separate species.

Riverside Tyrant (Knipolegus orenocensis).—This species was first observed and recorded 16–17 October 2008 (DCA, MGH, GFS, BMW), when up to five individuals were present on an island at the mouth of the Tambo River. MGH recorded and collected a displaying male and observed a female just upriver in Junín Region on 24 July 2010. Five individuals were netted and collected on the island in the mouth of the Tambo River on 6 July 2011. This species is known in Peru only from along the Amazon and lower Marañon rivers in Loreto Region. These are the first records from Ucayali and Junín Regions and constitute a range extension of 600 km.

Yellow-throated Flycatcher (Conopias parvus).—This species was fairly common at Otorongo and the Cohengua Stunted Forest and uncommon at Carachao between 29 May–15 June 2011. We obtained audio recordings and five specimens. This species is known in Peru from Loreto Region, particularly in areas with nutrient poor soils. These are the first records for Ucayali Region.

Crested Becard (Pachyramphus validus).—One female was collected at Otorongo on 15 June 2011 (RST). This species is resident along the eastern slopes of the Andes (*P. v. audax*) and an austral migrant to southeastern-most Peru (*P. v. validus*). Although not identified to subspecies, this individual was likely of the migrant form, and represents a first record for Ucayali Region.

Citron-bellied Attila (Attila citriniventris).—This species was fairly common at Otorongo and the Cohengua Stunted Forest and uncommon at Carachao between 25 May–15 June 2011. We obtained audio recordings and three specimens. This species is known in Peru only from Loreto Region, particularly in areas with nutrient-poor soils. These are the first records for Ucayali Region and constitute a range extension of 450 km.

Black Manakin (Xenopipo atronitens).—We found this species to be fairly common in short scrub <5 m in stature at the Cohengua Stunted Forest. We obtained audio recordings and collected four individuals. This species is patchily distributed in *varillales* throughout the Amazon Basin, but in Peru is known only from Jeberos in Loreto Region and Pampas del Heath in Madre de Dios Region. These are the first records for Ucayali Region.

Green Oropendola (Psarocolius viridis).—One individual was observed by BMW and MGH at Misión Unine on 8 January 2008, and three individuals were collected, two by LAAL and one by WAGB, at Quebrada Sipiria between 11–31 August 2009. Prior records from central Peru are few, but these additional records at different times of year suggest the presence of a population rather than isolated wanderers.

DISCUSSION

Our results represent the first inventory of the upper Ucayali River aside from the work of the Olalla brothers in 1927–1928. With the addition of 30 species that they recorded but were not recorded during our work (online Supplemental Material), the bird list for the upper Ucayali River would total 594 species. Locality information associated with the Olalla specimens has been questioned in the past, but recent re-examination of their specimens suggests that erroneous data can be isolated to a few portions of their collections (Wiley 2010). Specimens acquired by AMNH with the collections of Harvey Bassler, for example, are labeled

erroneously (and are not included in the online Supplemental Material). Specimens collected by Alfonso Olalla in March 1928 were labeled with the locality "Lagarto" from the right bank, but no location report was sent for this period and it is possible he was collecting on both banks. This possibility is supported by the presence in this collection of several species that we found only on the left bank (online Supplemental Material). Overall, however, there are few discrepancies between our results and the Olalla specimens. Our results support the assertion (Wiley 2010) that the Olalla data, with the exceptions mentioned above, are largely accurate.

The results of our inventory work, combined with prior information on bird distributions in nearby areas, suggest that the upper Ucayali River is a less effective barrier to species distributions than is the middle Ucayali River. This pattern is likely because of the greater ease with which birds might move across the narrow upper Ucayali River and its tributaries relative to the wider middle Ucayali River. Passive transport, the transfer of land and organisms from one side of the river to the other because of changes in the course of the river, may also play a role. The Ucayali has a history of frequent shifts within its alluvial plain, particularly along the lower stretches in the Pacaya-Samiria region (Lathrap 1968, Dumont 1991). These shifts may have been responsible for the movement of animal populations across the lower Ucayali River (Tuomisto and Ruokolainen 1997), and similar passive transfers may be responsible for the occurrence of some bird species on the "wrong" side of the upper Ucayali River.

With the decreased efficacy of the upper Ucayali as a barrier comes the potential for contact, hybridization, and introgression between geographic replacements. We found 20 pairs of taxa with largely allopatric or parapatric distributions in close proximity in the region of the upper Ucayali River, and possible intergrades or hybrids between three of those taxon pairs. It is likely both of these numbers are conservative estimates. We were only able to detect divergent forms for taxa from which we had sufficiently large samples (of observations, recordings, or specimens). Many of the taxa that potentially come into contact here are cryptic and difficult to separate, even in the hand. In addition, our sampling did not extend above the confluence of the Ucayali River with the Tambo and Urubamba rivers, where the potential for observing intergradation may be even higher. Genetic work also promises to provide a clearer picture of the number of contact zones and the extent of introgression between closely related taxa in this region. Recent work in other headwaters regions has begun to uncover instances of interbreeding between geographic replacements (Naka et al. 2012). It seems likely that, as more work is done in Amazonian headwaters, more zones of contact and cases of introgression and hybridization will be discovered.

The upper Ucayali River lies at the confluence of major Amazonian avifaunas. Parker et al. (1996) divided the Amazon into northern and southern regions, and we found that the avifauna of the upper Ucayali River shares affinities with both. Cracraft (1985) further divided the Amazon into smaller areas of endemism, and the upper Ucayali River lies near the confluence of two such areas - the Napo and Inambari. The delineation of the northern and southern Amazon, as well as the Napo and Inambari areas of endemism, is complicated, however, by the biogeographic complexity of the upper Ucayali River and nearby regions in the northern and central Peruvian Amazon. Although the boundary between areas is often ascribed to the Marañon River in northern Peru, many distributional limits in the region occur elsewhere, including at the Ucayali River, the Pachitea River, the Cordillera Azul, the Huallaga River, and in some cases in areas with no obvious landscape feature to serve as a barrier (Schulenberg et al. 2006b, 2010). The disparity in the locations of distributional limits is likely because of the absence of a single major barrier in this region, and is consistent with observed patterns in distributional limits between taxa and phylogeographic groups in other headwaters regions (Bates et al. 2004, Naka et al. 2012). The presence and positions of distributional limits in northern and central Peru have likely been determined by the cumulative effects of many landscape features, perhaps in conjunction with the effects of competition with Andean taxa (Terborgh and Weske 1975) or historical effects resulting from forest retraction (Haffer 1969), shifts in river courses (Sick 1967), downward influxes of montane habitats (Bush 1994), or the dynamic nature of the history of range expansion, contraction, and local extinction of each species (Brumfield 2012).

The avian diversity of the upper Ucayali River is likely at least partly attributable to the high diversity of habitats in the region. Many Amazonian habitats important to birds are present in the

region, including some with restricted distributions, such as stunted forest, bamboo, and river islands. These habitats both contribute to overall diversity, and provide important habitat for specialists, some of which are of conservation concern.

Successional habitats are of particular interest in the upper Ucayali Valley because they have been heavily influenced by human activity. Open areas have likely increased as a result of colonization and human expansion, and this trend may be driving the appearance of a number of species described above that have been considered rare or local in the Amazon Basin. Burrowing Owl in particular may be a recent colonist of the Peruvian Amazon, but other species may soon follow. Successional areas are important not only to residents arriving from elsewhere, but also to boreal and austral migrants. We recorded a high diversity of migrants in successional and edge habitats, and it seems likely these species will be influenced, as well as forest interior species, as deforestation continues.

The extraction of timber, petroleum, and gold, as well as deforestation for human habitation and farming, threaten the forests and other habitats of the upper Ucayali River. Conflict between indigenous groups, colonists, and corporations creates a difficult environment for conservation efforts regionally. The upper Ucayali warrants conservation not only for its avian diversity, but also for its biogeographic complexity and potential as a natural laboratory for evolutionary research.

ACKNOWLEDGMENTS

We thank the Ashéninka communities of the Organización Indigena Regional de Atalaya and Asociación Regional de Pueblos Indígenas, the Ashéninka community of La Selva, and the Shinipo-Conibo community of Amaquiria for their support. We thank especially our local guides for their committed assistance and protection. The Consorcio Forestal Amazónico provided access and logistical support. We are very grateful to R. H. and M. Wiley for sharing their carefully collected data on the Olalla specimens at the American Museum of Natural History. G. F. Budney (ML) and D. L. Dittmann and S. W. Cardiff (LSUMNS) were generous in support of logistical aspects of the collecting and recording efforts. I. J. Lovette, J. W. Fitzpatrick, J. P. O'Neill, and D. W. Winkler provided encouragement early during the project. M. J. Miller provided helpful unpublished data on bird distributions. T. S. Schulenberg, D. F. Lane, and M. L. Isler gave generously of their extensive knowledge of the Peruvian avifauna. J. V. Remsen, R. T. Brumfield, T. H. Valqui, J. M. Bates, and J. L. Cracraft provided financial, logistical, and intellectual support throughout. M. L. Isler, M. B. Robbins, R. H. Wiley, J. V. Remsen, and R. T. Brumfield provided helpful comments on the manuscript. We thank the Dirección General Forestal y de Fauna Silvestre (DGFFS) of Peru for permission to collect in the region (Reserva Comunal El Sira N° 001-2009, RD N°0345-2010, RD N°0281-2011). Thanks to D. Mishari, Chief of the Reserva Comunal El Sira, for facilitating permission to work within the Reserve. Funding and support for fieldwork were provided by the National Geographic Society, Cornell Laboratory of Ornithology, National Science Foundation (grant DEB-0841729 to Robb T. Brumfield), Explorer's Club, Cornell Presidential Research Scholars, Jordani Zoology Club, Eastern Mountain Sports, H. B. Conover Fund and the Ornithological Research Fund of the Field Museum's Bird Division, and the American Museum's F.M. Chapman Memorial and L. J. and L. C. Sanford Funds.

LITERATURE CITED

Barlow, J., T. Haugasen, and C. A. Peres. 2002. Sympatry of the Black-faced Hawk and White-browed Hawk in the lower Rio Tapajós, Pará, Brasil. Cotinga 18:77–79.

Bates, J. M., J. Haffer, and E. Grismer. 2004. Avian mitochondrial DNA sequence divergence across a headwater stream of the Rio Tapajós, a major Amazonian river. Journal of Ornithology 145:199–205.

Brumfield, R. T. 2012. Inferring the origins of lowland Neotropical birds. Auk 129:367–376.

Bush, M. B. 1994. Amazonian speciation: a necessarily complex model. Journal of Biogeography 21:5–17.

Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithological Monographs 36:49–84.

Dickinson, E. C. 2003. The Howard and Moore complete checklist of birds of the world. Christopher Helm, London, UK.

Dickinson, E. C. and J. V. Remsen, Jr. 2013. The Howard and Moore complete checklist of birds of the world. Volume 1: non-passerines. Aves Press, Eastbourne, UK.

Dumont, J.-F. 1991. Cambio del curso de los ríos Marañon y Ucayali en la depresión Ucamara durante el Cuaternario Reciente. Pages 483–487 *in* Volumen de Resúmenes Extendidos, VII Congreso Peruano de Geologia, Lima, Peru.

González M, O. E. 1998. Birds of the lowland forest of Cerros del Sira, central Peru. Cotinga 9:57–60.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165:131–137.

Haffer, J. 1992. On the "river effect" in some forest birds of southern Amazonia. Boletim do Museu Paraense Emílio Goeldi, Zoologia 8:217–245.

Harvey, M. G., B. M. Winger, G. F. Seeholzer, and D. Cáceres A. 2011. Avifauna of the Gran Pajonal and southern Cerros del Sira, Peru. Wilson Journal of Ornithology 123:289–315.

Hinkelmann, C. 1996. Systematics and geographic variation in Long-tailed Hermit hummingbirds, the *Phaethornis superciliosus-malaris-longirostris* species group (Trochilidae), with notes on their biogeography. Ornitologia Neotropical 7:119–148.

ISLER, M. L., P. R. ISLER, B. M. WHITNEY, K. J. ZIMMER, AND A. WHITTAKER. 2009. Species limits in antbirds (Aves: Passeriformes: Thamnophilidae): an evaluation of *Frederickena unduligera* (Undulated Antshrike) based on vocalizations. Zootaxa 2305:61–68.

KRATTER, A. W. 1997. Bamboo specialization by Amazonian birds. Biotropica 29:100–110.

LATHRAP, D. W. 1968. Aboriginal occupation and changes in river channel on the central Ucayali, Peru. American Antiquity 33:62–79.

NAKA, L. N., C. L. BECHTOLDT, L. M. P. HENRIQUES, AND R. T. BRUMFIELD. 2012. The role of physical barriers in the location of avian suture zones in the Guiana Shield, northern Amazonia. American Naturalist 179:E115–E132.

O'NEILL, J. P. 1969. Distributional notes on the birds of Peru: including twelve species previously unreported from the republic. Occasional Papers of the Museum of Zoology, Louisiana State University 37:1–11.

O'NEILL, J. P., C. A. MUNN, AND I. FRANKE. 1991. *Nannopsittaca dachilleae*, a new species of parrotlet from eastern Peru. Auk 108:225–229.

O'NEILL, J. P. AND T. A. PARKER III. 1997. New subspecies of *Myrmoborus leucophrys* (Formicariidae) and *Phrygilus alaudinus* (Emberizidae) from the upper Huallaga Valley, Peru. Ornithological Monographs 48:485–491.

O'NEILL, J. P. AND D. L. PEARSON. 1974. Preliminary studies of the birds of Yarinacocha, Departamento de Loreto, Perú. Publicaciones del Museo de Historia Natural "Javier Prado", Zoologia Serie A 25:1–13.

OFICINA NACIONAL DE EVALUACIÓN DE RECURSOS NATURALES. 1968. Inventario, evaluación, e integración de los recursos naturales de la zona del Río Tambo-Gran Pajonal. ONERN, Lima, Peru.

PARKER III, T. A., D. F. STOTZ, AND J. W. FITZPATRICK. 1996. Ecological and distributional databases. Pages 113–436 *in* Neotropical birds: ecology and conservation (D. F. Stotz, J. W. Fitzpatrick, T. A. Parker III, and D. Moskovits, Editors). University of Chicago Press, Chicago, USA.

RAPOSO DO AMARAL, F. S., L. F. SILVEIRA, AND B. M. WHITNEY. 2007. New localities for Black-faced Hawk south of the Amazon River and the description of the immature plumage of the White-browed Hawk. Wilson Journal of Ornithology 119:450–454.

REMSEN, J. V., C. D. CADENA, A. JARAMILLO, M. NORES, J. F. PACHECO, J. PÉREZ-EMÁN, M. B. ROBBINS, F. G. STILES, D. F. STOTZ, AND K. J. ZIMMER. 2013. A classification of the bird species of South America. American Ornithologists' Union, Waco, TX, USA. www.museum.lsu.edu/~Remsen/SACCBaseline.html (accessed 3 Jan 2014).

RIDGELY, R., T. ALLNUTT, T. BROOKS, D. MCNICOL, D. MEHLMAN, B. YOUNG, AND J. ZOOK. 2003. Digital distribution maps of the birds of the Western Hemisphere. NatureServe, Arlington, VA, USA.

RIDGELY, R. S. AND G. TUDOR. 1989. The birds of South America. Volume I, the Oscine passerines. University of Texas Press, Austin, USA.

ROSENBERG, G. H. 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru. Condor 92:427–443.

SCHULENBERG, T. S. 2001. Avifauna of the northern Cordillera de Vilcabamba, Peru *in* Biological and social assessments of the Cordillera de Vilcabamba, Peru (L. E. Alonso, A. Alonso, T. S. Schulenberg, and F. Dallmeier, Editors). Conservation International, Washington, D.C., USA.

SCHULENBERG, T. S., C. ALBUJAR, AND J. I. ROJAS. 2006a. Birds *in* Rapid biological inventories - Perú: Sierra del Divisor (C. Vriesendorp, T. S. Schulenberg, D. Moskovits, and J. Rojas, Editors). Field Museum, Chicago, USA.

SCHULENBERG, T. S., D. F. STOTZ, AND L. RICO. 2006b. Distribution maps of the birds of Peru, version 1.0. Environment, Culture, and Conservation (ECCo), Field Museum, Chicago, USA. fm2.fieldmuseum.org/uw_test/birdsofperu (accessed 2 Jan 2014).

SCHULENBERG, T. S., D. F. STOTZ, D. F. LANE, J. P. O'NEILL, AND T. A. PARKER III. 2010. Birds of Peru: revised and updated edition. Princeton University Press, Princeton, NJ, USA.

SHRUM, P. L., W. W. BOWERMAN, D. G. OLAECHEA, AND R. AMABLE. 2011. More records of sympatry of Black-faced Hawk (*Leucopternis melanops*) and White-browed Hawk (*L. kuhli*) in Madre de Dios, Peru. Journal of Raptor Research 45:104–105.

SICK, H. 1967. Rios e enchentes na Amazônia como obstáculo para a avifauna. Pages 495–520 *in* Atas do Simpósio sobre a Biota Amazônica. Volume 5. Conselho Nacional de Pesquisas, Rio de Janeiro, Brazil.

SOCOLAR, S. J., Ó. GONZÁLEZ, AND G. FORERO-MEDINA. 2012. Noteworthy bird records from the northern Cerros del Sira, Peru. Cotinga 35:24–36.

SRINIVAS, A. AND J. MOLINA VILCA. 2013. New distributional records of Rufous-necked Puffbird *Malacoptila rufa* and Pearly Antshrike *Megastictus margaritatus* in Peruvian Amazonia. Cotinga 35:88–89.

TERBORGH, J. AND J. S. WESKE. 1975. The role of competition in the distribution of Andean birds. Ecology 56:562–576.

TUOMISTO, H. AND K. RUOKOLAINEN. 1997. The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. Biodiversity and Conservation 6:347–357.

WALLACE, A. R. 1852. On the monkeys of the Amazon. Proceedings of the Zoological Society of London 20:107–110.

WESKE, J. S. 1972. The distribution of the avifauna in the the Apurimac Valley of Peru with respect to environmental gradients, habitat, and related species. Dissertation. University of Oklahoma, Norman, USA.

WHITNEY, B. M., D. C. OREN, R. T. BRUMFIELD, AND P. STOUFFER. 2004. A new species of *Thamnophilus* antshrike (Aves: Thamnophilidae) from the Serra do Divisor, Acre, Brazil. Auk 121:1031–1039.

WILEY, R. H. 2010. Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. Bulletin of the American Museum of Natural History 343: 1–68.

ZIMMER, J. T. 1950. Studies of Peruvian birds. Number 55, the hummingbird genera *Doryfera*, *Glaucis*, *Threnetes*, and *Phaethornis*. American Museum Novitates 1449: 1–51.

The Wilson Journal of Ornithology 126(2):192–206, 2014

150 YEARS OF CHANGES IN BIRD LIFE IN CAMBRIDGE, MASSACHUSETTS FROM 1860 TO 2012

MICHAEL W. STROHBACH,[1,3,4] ANDREW HRYCYNA,[2] AND PAIGE S. WARREN[1]

ABSTRACT.—The process of urbanization and its effects on birds has rarely been documented over long time periods. One exception is a bird count started in the 1860s, when the American ornithologist William Brewster first recorded all the bird species on his property in Cambridge, Massachusetts. Since then, invasive species such as the House Sparrow (*Passer domesticus*) have been introduced, and the site transformed from an estate surrounded by farmland on the rural edge of the city to a residential neighborhood in the inner core of the Boston metropolitan area. We are fortunate to have additional bird species accounts from around 1900, 1940, 1950, and 1960. In 2012 we repeated the bird survey, thus expanding the time series to 150 years. The changes in the bird community over time have been profound and the data contain a wealth of "stories" about how different species and species guilds have coped. The transition from an agricultural to an urban but also more forested system is clearly visible in the records. Overall, species richness has declined from 26 species in the 1860s to just 12 in 2012. However, this is a slight increase from the low point in the 1960s, and there is evidence that some conditions for birds have improved in the last 50 years. *Received 16 August 2013. Accepted 14 December 2014.*

Key words: community composition change, eBird, habitat change, land-cover/land-use change, long-term data, suburban/urban birds, urbanization.

The impact of urbanization on bird communities has rarely been documented over time. Most of what we know today about how urbanization influences birds stems from "space-for-time" studies across urban regions and along rural-urban gradients (Marzluff et al. 2001). In such studies, different levels of urban development in space, for example from the city center to the rural hinterland, are assumed to mirror urbanization over time (see reviews by Marzluff et al. 2001, Chace and Walsh 2006, Pickett et al. 2011, Shanahan et al. 2014). Rarely do bird surveys span several years or even decades, and only a few actually span a century-long time period (Marzluff et al. 2001). One example is the Christmas Bird Count that started in 1900 and is one of the oldest and largest wildlife surveys in the world (Butcher et al. 1990). However, the Christmas Bird Count aggregates over large areas (24 km radius), therefore blending rural and urban areas. Other examples are the changes reported by Batten (1972) for an area near London, UK, between 1830 and 1970, and by Shultz et al. (2012) for the bird community of the University of California-Berkeley campus, USA, between 1913 and 2007. In a different approach, Major and Parson (2010) used museum specimens to reconstruct the pre-1900 bird community of Sydney, Australia, and compared it to a contemporary survey.

In New England, a series of bird surveys was started in 1860 by ornithologist and co-founder of the American Ornithologists' Union, William Brewster, on his family property in Cambridge, Massachusetts (Brewster 1906). It was repeated in 1900, and continued on a neighboring property by Charles F. Walcott in 1940–1943, 1953–1955 and 1960–1964 (Walcott 1959, 1974). The surveys together document the changes in the avifauna as the area transformed from estates surrounded by farmland on the rural edge of the city to a residential neighborhood in the inner core of the Boston metropolitan area. During that time, the city of Cambridge grew from ~26,000 inhabitants in 1860 to over 120,000 in 1950 (Gibson 1998). The changes in the bird community were quite substantial: the number of breeding species decreased from 26 in the 1860s to nine in the early 1960s (Walcott 1974). Brewster and Walcott attributed the observed changes mainly to habitat loss resulting from urbanization, the introduction of invasive species, and pesticide spraying starting in the early 20th century.

All three aspects have been shown to influence bird communities elsewhere. Bird richness often

[1] Department of Environmental Conservation, University of Massachusetts – Amherst, Amherst, MA 01003, USA.

[2] Sustainability and Environmental Management Graduate Program, Harvard University Extension School, Cambridge, MA, USA.

[3] Current address: Humboldt Universität zu Berlin, Department of Geography, Landscape Ecology Laboratory, Unter den Linden 6, 10099 Berlin, Germany.

[4] Corresponding author;
e-mail: michael.strohbach@geo.hu-berlin.de

decreases along rural-urban gradients or shows a unimodal distribution, with low levels in rural and urban areas, and highest richness at intermediate urbanization levels (Chace and Walsh 2006, Tratalos et al. 2007, Shanahan et al. 2014). In any case, lowest levels can always be found at highest building densities (Chace and Walsh 2006, Tratalos et al. 2007, Shanahan et al. 2014). Highly urbanized areas are often dominated by non-native species and non-specialist species, and few insectivore species can be found. In addition, non-migratory species and populations of partially migratory species are favored because of better overwintering conditions compared with rural areas (White et al. 2005, Chace and Walsh 2006, Devictor et al. 2006, Evans et al. 2010, Shanahan et al. 2014). Habitat loss and habitat change is often correlated with loss of species (Shanahan et al. 2014). While the impacts of outright habitat loss are obvious, the underlying mechanisms between species loss and habitat change are not well understood and often multilayered (Shrubb 2003, Shochat et al. 2010, Shanahan et al. 2014). For pesticides, the harmful effects on birds, including direct poisoning, loss of fertility, reduced breeding success, and loss of prey resources, are well documented (Wallace et al. 1961, Fry 1995).

Little is known about the changes in bird life that have happened in Cambridge since 1964. Therefore, we have revisited Brewster and Walcott's original sites and continued the bird surveys, thus expanding the time series to 150 years. In addition, we discuss changes in richness and life history traits of the breeding bird community in the light of contemporary findings from urban ecology that were not available to Brewster and Walcott. Using historic maps, we have assessed the urban development that occurred at the sites since 1873. From historic aerial photos we have estimated changes in tree cover since 1951. For a nearby reference site that Walcott surveyed in the 1940s and again in the 1960s, we obtained records from the eBird online database of bird distribution and abundance (eBird 2013). Considering that Cambridge was already a densely developed city in the 1960s, we predicted that the bird community would have stabilized between then and 2012.

Although the data provide a unique window into the past, interpretation and generalization are challenging, because the small number of study sites and limited number of repetitions of the historical surveys do not allow for statistical comparisons between sampling periods. Nevertheless, the observations represent a real sample of the bird communities of Cambridge at the respective time periods, and general trends over the course of 150 years are unlikely to be the result of chance. We explore the ways in which documenting changes in the bird communities over time corresponds to and differs from conclusions reached through "space-for-time" analyses.

METHODS

Study Area

Cambridge is located at the Massachusetts Bay in the northeastern USA (42° 22′ N, 71° 06′ W). The settlement was established in 1630 and preserved a rural character even until 1846 when it was incorporated as a city (Cambridge Historical Commission 2012). Between 1860–1950, the population more than quadrupled from 26,000 inhabitants to >120,000 (Gibson 1998). Today, the city has about 105,100 inhabitants and a population density of 6,359 inhabitants per km^2 (U.S. Census Bureau 2012). Fifteen percent of Cambridge is covered by open space (open space layer from Commonwealth of Massachusetts 2012) and canopy cover is 30% (O'Neil-Dunne 2012). The sites studied by Walcott and Brewster are located west of the historic center of Cambridge, ~350 m north of the Charles River. Fresh Pond Reservation is located ~1 km to the northwest (Fig. 1).

Reconstruction of Site Locations, Urban Development and Tree Canopy Cover.—Neither Brewster nor Walcott provided maps of their study sites. Therefore, we used descriptions by Brewster (1906) and Walcott (1974) and historic maps to locate them. The Brewster family property, referred to as *Site A* in this paper, was located on the intersection of Brattle and Sparks Streets (Brewster 1906). It is well marked as the property of J. Brewster, William Brewster's father, on an 1873 atlas (Hopkins 1873) from which the boundary was digitized in a Geographical Information System (ESRI ArcGIS 10.1). Charles F. Walcott's property was located ~140 m north of Brewster's on the intersection of Sparks Street and Huron Avenue (Walcott 1974). The property is marked as the property of Anna M. Walcott and Charles Walcott in the 1916 atlas (Bromley and Bromley 1916) in which it was also digitized. The site is referred to as *Site B* in

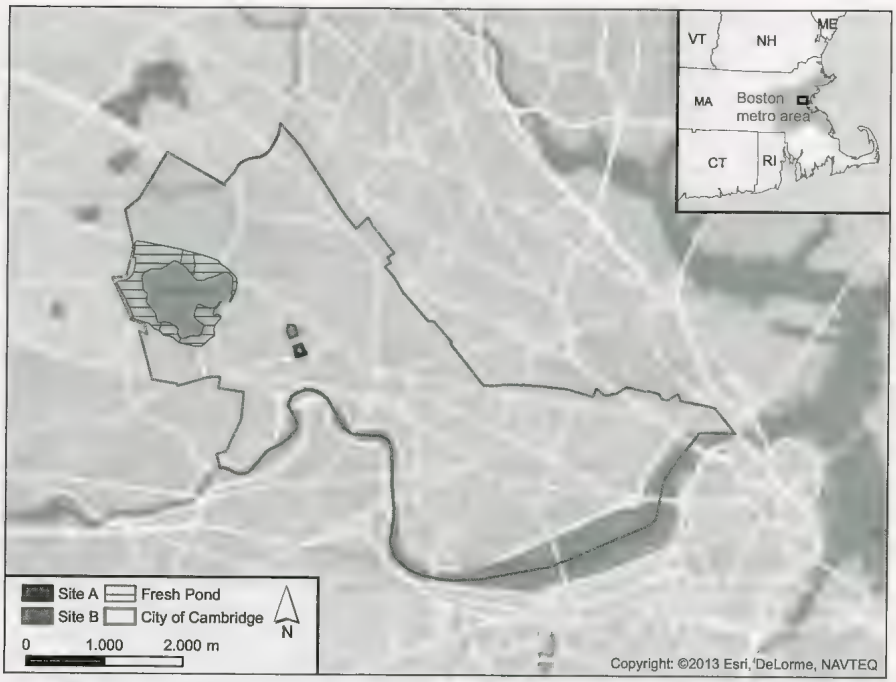


FIG. 1. Location of two residential study sites A and B, and Fresh Pond Reservation in Cambridge, Massachusetts. Base map © ESRI, DeLorme, NAVTEQ.

this paper. According to Walcott (1974), both sites are "about six acres" (2.43 ha) in size. The actual areas that we digitized from the property maps are slightly smaller: Site A is 2.12 ha; Site B 1.93 ha.

To get an estimate of urban development, houses and roads were digitized for both sites from historic and contemporary maps (Hopkins 1873, Insurance maps of Cambridge Massachusetts 1900, Atlas of the city of Cambridge Massachusetts 1930, Insurance maps of Cambridge Massachusetts 1962, ESRI World Topographic Map Service 2012). The earliest available summer aerial photos date to 1951 and were scanned from the library collection of the University of Massachusetts – Amherst. We orthorectified them in ESRI ArcGIS 10.1, based on 2010 aerial photos (provided by the city of Cambridge IT Dept.), and digitized tree canopy on sites A and B. Likewise, the 1971 aerial photos were accessed and processed. Finally, the current canopy cover was digitized using the city of Cambridge LIDAR scan from 2009 and the 2010 imagery (provided by the city of Cambridge IT Dept.).

Site A (William Brewster's Site).—William Brewster's house dates back to colonial times but was moved and expanded since then (Daughters of the American Revolution 1907). In 1860–1873, when Brewster began recording birds, the streets along the gently sloping property were lined with tall elms and lindens. Behind the house there was a flower and vegetable garden, an apple and pear orchard, rows of berry bushes, mowing fields and a small pasture for cows and horses. The neighboring estates were of similar character and open farmland stretched west and north (Brewster 1906).

As Cambridge grew rapidly in the late 19th and early 20th century, the property was subdivided and several houses were built, as can be seen on the map from 1900 (Fig. 2). When Brewster recorded the birds for the second time in 1900–1904, what remained of the property contained an old flower garden and some lawn shaded by a few large trees. Of the orchards, only four apple trees

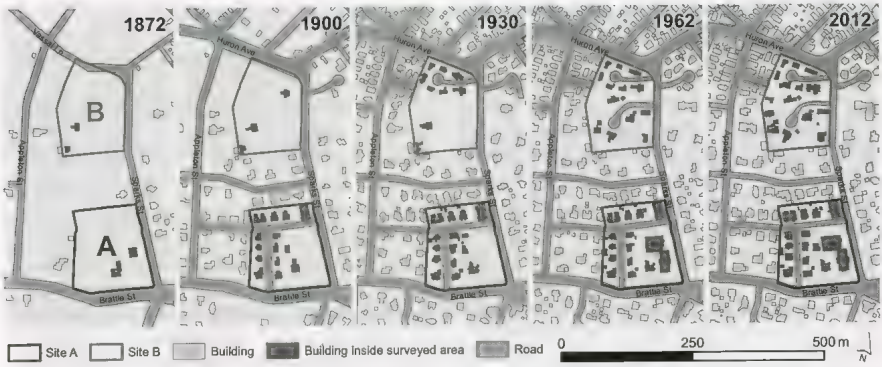


FIG. 2. Housing development between 1872 and 2012 at the two residential study sites A and B in Cambridge, Massachusetts. Maps were digitized from Hopkins 1873, Insurance maps of Cambridge Massachusetts 1900, Atlas of the city of Cambridge Massachusetts 1930, Insurance maps of Cambridge Massachusetts 1962, and ESRI World Topographic Map Service 2012.

remained, and the pear orchard had been thickly planted with forest trees in 1886. Brewster designed the property as an "artificial woodland" with an eye to attracting birds by selecting certain herbaceous and woody plants, constructing two ponds for water supply, and excluding cats. No farmland remained nearby and the closest large open space was Fresh Pond Reservation. However, the area had more tree cover than previously (Brewster 1906).

After 1904, the only major development of the property happened in the early 1960s, when a church was built (Fig. 2). Today, Brewster's house belongs to the church and the property is landscaped with lawns, trees, and bushes. Otherwise, Site A is residential with mainly two story houses, small gardens and large trees.

Site B (Charles F. Walcott's Site).—Charles F. Walcott moved the study site to his property, ~140 m north of Brewster's. At the time of his first survey in the 1940s, he describes it as "pleasingly variegated" and as being covered with a thick tangle of berry bushes, shrubs, and trees. It also contained an old apple and pear orchard (Walcott 1974, Fig. 2).

At the time of Walcott's second bird monitoring in the mid 1950s, 1.6 ha of the property were subdivided. What remained in 1960–1964 still contained shrubs and trees as well as parts of the pear orchard. Between 1962–2012, only a few houses were built. The area is entirely residential with one and two story houses, surrounded by gardens and large trees. Site B remains less densely built up than Site A (Fig. 2).

Fresh Pond Reservation.—Fresh Pond Reservation (Fig. 1) was used by Walcott (1974) as a nearby comparison site with "a variety and amount of natural habitat" comparable to the residential section of Cambridge in the 1860s and exempt from insect spraying. In fact, Fresh Pond has had a complicated history of land use in the period since Brewster's time. In the 19th century, Fresh Pond was used for both industry and recreation, surrounded by miles of marshes and swamps, later to be filled and developed. The city of Cambridge made Fresh Pond its municipal reservoir in 1888, creating a reservation of public land, partially following plans by the Olmsted Brothers landscape design firm. Today, the reservation is 66 ha, surrounded by major traffic arteries and highly developed commercial and residential areas (Sinclair 2009).

Bird Sampling

Sites A and B.—William Brewster recorded all the nesting pairs of birds he observed around his house for the periods of 1860–1873 and 1900–1904. In addition, he recorded birds as "transient" when they were observed on the property during the breeding season, but no indication of nesting was found. Likewise, Charles F. Walcott recorded the nesting and transient bird species on his property for the periods of 1940–1943, 1953–1955, and 1960–1964.

None of the authors of the present study had the advantage of living on either of the sites, so in 2012 we conducted a focused survey. We contacted all the property owners to inform them about our project and to obtain permission to access their property. Permissions were provided for 63% of the property area of Site A and 49% of Site B, and from these properties and from public roads, the sites were almost entirely visible. We subdivided both sites into 10 quadrants of roughly equal size. Both sites were mapped on six mornings between 0500–1000 Eastern Daylight Time (EDT) and between June 6th and July 8th. We slowly moved through the sites and recorded the number of birds seen or heard by time, site, and quadrant, and noted aspects of behavior that indicated breeding (see below). An average of 75 min were spent on each site. We alternated the starting location for the bird counts between Site A and Site B to avoid a time bias.

Unlike Walcott and Brewster, we could not spend the whole season at the sites and obtain a full confirmation of breeding. We therefore adopted an established protocol for assigning breeding status from the Massachusetts Breeding Bird Atlas 2 (Mass Audubon 2008). The protocol includes four breeding categories: *observed*, which refers to birds observed during the breeding season but not in suitable nesting habitat; *possible*, which refers to birds observed during the breeding season and in suitable habitat, but without further indication of breeding; *probable*, which refers to birds observed during the breeding season and in suitable habitat, and with some indication of breeding, e.g., a territory presumed through song at same location on at least two occasions 7 days (or more) apart; and *confirmed*, which refers to birds observed during the breeding season and in suitable habitat, and with clear signs of breeding, e.g., adult seen sitting on nest or carrying nesting material (see Mass Audubon 2008 for full protocol).

To compare our results with the historic data, we classified *observed* and *possible* species as transients and *probable* and *confirmed* species as nesting. We created species accumulation curves of the nesting species to test whether our sampling effort was sufficient. Species accumulation curves were compiled according to Colwell et al. (2004), using the function *specaccum* of the *R* package *vegan* (Oksanen et al. 2011).

Fresh Pond Reservation.—Unfortunately, William Brewster limits his observations of Fresh Pond birds to waterfowl (Brewster 1906), but Walcott (1974) provides species lists for transient and nesting bird species observed in June for the time periods of 1940–1944 and 1960–1964. In 2012, a full breeding bird survey of an area as big as Fresh Pond Reservation (66 ha) was not possible. However, Fresh Pond Reservation is a common birding location and well represented in the eBird online database of bird distribution and abundance (eBird 2013). Three "Birding Hotspots" are located within the Reservation: *Fresh Pond*, *Fresh Pond–Black's Nook*, and *Fresh Pond–Lusitania Meadow* (eBird 2013). Fresh Pond–Black's Nook was systematically surveyed in 2012 and reported in Hrycyna (2013) as well as eBird (2013). We obtained the June records from the three "Birding Hotspots" for the years 2008–2012. Breeding status was not assessed, because records in eBird do not typically contain enough behavioral detail to evaluate likelihood of nesting.

Life History Traits

To characterize the changes in the bird community of Cambridge, we analyzed information on food, nesting and habitat preferences, all of which have been shown to be affected by urbanization (DeGraaf and Wentworth 1986, White et al. 2005, Chace and Walsh 2006, Devictor et al. 2006, Major and Parson 2010, Shanahan et al. 2014). Food and nesting preferences were derived from DeGraaf and Wentworth (1986). If different food sources were used throughout the year, we selected the one used during the breeding season. Habitat preferences were derived from DeGraaf and Yamasaki (2001) who describe natural history profiles of wildlife species in New England. In order to examine the community response to the loss of open habitat and forest re-growth, we focused on the individual species' ability to utilize two contrasting habitat types: open agricultural landscapes that were abundant in the 19th century, represented by *upland field* and *orchard* habitats (Brewster 1906); and the forest habitats that would likely cover the area today in the absence of urban development, namely *southern hardwood* and *oak-pine* habitats (DeGraaf and Yamasaki 2001), only focusing on *sawtimber* and *large sawtimber* successional stages. By emphasizing the ends of this open habitat to forest gradient, we ensured that we identified true specialists for either open or forest habitat.

Challenges of the Legacy Data

So-called legacy datasets, such as the ones gathered by Brewster and Walcott, have been highly beneficial for scientific research (Marzluff et al. 2001), but although the ornithological knowledge of both authors is undisputed, there are several challenges.

(1) The sampling lacks a protocol and standardization of sampling effort. The first sampling period covers 13 years, whereas the others cover between 2–4 years. This could have an influence on the reported species numbers. We address this issue by just focusing on the nesting species, because they are less likely to vary inter-annually than transient species.

(2) Walcott shifted the study site from Brewster's, which makes the interpretation of the changes between 1904–1940 challenging. In 2012, we addressed this issue by sampling both sites.

(3) Walcott is inconsistent in regard to reporting transient gulls and herons at Site B. They are included in 1959 but not in 1974. We therefore excluded these species from our sampling. There is also an inconsistency in the number of transient species reported in Walcott (1974) that could not be clarified by the Walcott's articles from 1953 or 1959. These issues are of minor importance, because we will focus mainly on nesting species.

(4) It is not clear how the targeted sampling design of 2012 compares to Brewster's and Walcott's records. The fact that we found more confirmed or probable nesting species in 2012 than Walcott reported in the 1960s (see results) suggests that we were not under-sampling. Conversations with residents engaged in bird watching also suggest that no common species is missing from our observations.

(5) It is not clear whether Brewster and Walcott were very stringent about their survey areas. We were able to clearly map the extent of both authors' original property from historic maps, but the authors don't mention explicitly whether they continued sampling all of their former property after it was subdivided. If they didn't, there could be some bias in the data caused by the biogeographical fact that smaller areas often support fewer species (e.g., Davis and Glick 1978). We address this issue by focusing on life history traits of the bird community and not just species richness.

RESULTS

Urban Development and Tree Canopy Cover.—The area occupied by houses and roads has continuously increased over the last 150 years in the study area, but the dynamics differ between the two sites (Figs. 2 and 4). On Site A, development occurred earlier and was more intense. Canopy cover has declined from 43% to 28% on Site A between 1951–1971 but almost fully recovered to 39% today. On Site B, canopy has steadily increased from 36% in 1951 to 55% today.

Bird Richness at Sites A, B, and Fresh Pond.—In 2012, a total of 21 species were observed on both residential sites, 18 on Site A and 18 on Site B (Table 1). Eight species on Site A and 12 species on Site B were assumed to be nesting. Species accumulation curves of nesting species indicate that most species were found (Fig. 3).

Both the numbers and the composition of nesting birds have changed between 1860–2012 (Table 1, Fig. 5). The number of nesting bird species has continuously declined on Site A, with the strongest decline between 1860–1873 and 1900–1904. On Site B, the number of nesting birds strongly declined between 1940–1943 and 1953–1955, slightly decreased in 1960–1964, and slightly increased in 2012. Of the 26 bird species nesting in the 1860s, only three were nesting on the sites during all survey periods: Gray Catbird (*Dumetella carolinensis*), Blue Jay (*Cyanocitta cristata*) and American Robin (*Turdus migratorius*). House Sparrows (*Passer domesticus*) have been reported since 1900–1904 and European Starlings (*Sturnus vulgaris*) and Black-capped Chickadees (*Poecile atricapillus*) since 1940–1943. American Goldfinches (*Spinus tristis*) were found to be nesting again in 2012 after having been transient in all but the first survey period. Five species have been nesting for the first time in 2012: Mourning Dove (*Zenaida macroura*), House Finch (*Haemorhous mexicanus*), Carolina Wren (*Thryothorus ludovicianus*), White-breasted Nuthatch (*Sitta carolinensis*) and the Common Grackle (*Quiscalus quiscula*).

At Fresh Pond Reservation, most of the species observed by Walcott can still be found (Table 2). However, an additional 33 species not observed by Walcott were recorded in eBird (2013).

Life History Traits.—The ratio of nesting insectivore species to omnivore species has continuously decreased on Site A. While insectivore

TABLE 1. Nesting (black) and transient (gray) species observed at Site A (cf., Figs. 1, 2) in 1860–1873 and 1900–1904 by Brewster (1906), at Site B in 1940–1943, 1953–1955, and 1960–1964 by Walcott (1959, 1974), and at both sites in 2012.

Species	1860–73	1900–04	1940–43	1953 55	1960–64	2012 Site A 2012 Site B
Hirundo rustica (Barn Swallow)						
Dolichonyx oryzivorus (Bobolink)						
Molothrus ater (Brown-headed Cowbird)						
Tachycineta bicolor (Tree Swallow)						
Passerina cyanea (Indigo Bunting)						
Sialia sialis (Eastern Bluebird)						
Archilochus colubris (Ruby-throated Hummingbird)						
Empidonax minimus (Least Flycatcher)						
Vireo gilvus (Warbling Vireo)						
Coccyzus americanus (Yellow-billed Cuckoo)						
Coccyzus erythropthalmus (Black-billed Cuckoo)						
Spizella passerina (Chipping Sparrow)						
Vireo flavifrons (Yellow-throated Vireo)						
Setophaga petechia (Yellow Warbler)						
Contopus virens (Eastern Wood-Pewee)						
Troglodytes aedon (House Wren)						
Tyrannus tyrannus (Eastern Kingbird)						
Melospiza melodia (Song Sparrow)						
Haemorhous purpureus (Purple Finch)						
Vireo olivaceus (Red-eyed Vireo)						
Icterus galbula (Baltimore Oriole)						
Quiscalus quiscula (Common Grackle)						
Bombycilla cedrorum (Cedar Waxwing)						
Spinus tristis (American Goldfinch)						
Chaetura pelagica (Chimney Swift)						
Colaptes auratus (Northern Flicker)						
Dumetella carolinensis (Gray Catbird)						
Cyanocitta cristata (Blue Jay)						
Turdus migratorius (American Robin)						
Pheucticus ludovicianus (Rose-breasted Grosbeak)						
Setophaga ruticilla (American Redstart)						
Megascops asio (Eastern Screech-Owl)						
Corvus brachyrhynchos (American Crow)						
Passer domesticus (House Sparrow)						
Falco sparverius (American Kestrel)						
Hylocichla mustelina (Wood Thrush)						
Chordeiles minor (Common Nighthawk)						
Sitta carolinensis (White-breasted Nuthatch)						
Picoides pubescens (Downy Woodpecker)						
Sturnus vulgaris (European Starling)						
Poecile atricapillus (Black-capped Chickadee)						
Cardinalis cardinalis (Northern Cardinal)						
Zenaida macroura (Mourning Dove)						
Haemorhous mexicanus (House Finch)						
Thryothorus ludovicianus (Carolina Wren)						
Baeolophus bicolor (Tufted Titmouse)						
Mimus polyglottos (Northern Mockingbird)						
# Nesting:	26	14	16	10	9	Site A: 8 Site B: 12

species originally were in the majority, by 1900–1904 their number was about equal to omnivore species and this pattern remains today (Fig. 5e). Site B showed a stronger decline in insectivore than in omnivore species between 1940–1963, and since 1953–1955 the majority of species are omnivore (Fig. 5f). However between 1963–2012, the number of insectivore species slightly increased.

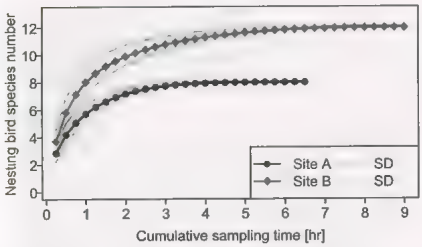


FIG. 3. Species accumulation curves of nesting birds for the two residential study sites A and B in Cambridge, Massachusetts. Species accumulation curves were compiled for 15-min time periods, and confidence intervals show standard deviation. Birding was carried out during six mornings in June and early July 2012.

Concerning preferred nesting sites, tree-nesting species were the largest group on Site A in the first two study periods, but cavity-nesting species are in the majority today (Fig. 5c). The pattern is different on Site B. In 1940–1943, cavity nesting species were the largest guild, followed by tree nesting species (Fig. 5d). In 1960–1964, the number of shrub-nesting species had increased and cavity-nesting species had declined, but only by one species in each case. This pattern remains the same through the current sampling period.

The preferred habitat has also changed. Birds that only utilize open habitat were the second most common species group in 1860–1873 but declined rapidly afterwards and were nearly absent after 1940–1943 (Fig. 5a, b). Birds utilizing only forest habitat were rare throughout the 150 years but showed highest numbers on Site B in the 1940s. Birds that can utilize both open and forested habitat were most common during all survey periods.

DISCUSSION

Habitat loss caused by urban development has certainly had a strong impact on species richness at the surveyed sites. Every major building period (between 1873–1900 on Site A and between 1943–1953 on Site B) was followed by a strong decline in nesting species number (Figs. 2 and 4, Table 1). Today, Brewster's Site A shows the highest intensity of development, and the number of nesting species is the lowest on record. Batten (1972) reported a similar decline following urbanization of an area north of London, UK, between 1830–1970. At the residential sites in Cambridge, the number of insectivore species has declined more strongly than omnivore species (Fig. 5e). The number of small insectivore species also appears to have been reduced mostly by 100 years of urbanization in Sydney, Australia (Major and Parson 2010). The decline in species richness and the loss of specialized bird guilds is commonly found in "space-for-time" analyses of birds' responses to urbanization (e.g., Chace and Walsh 2006, Devictor et al. 2006, Shanahan et al. 2014).

At Fresh Pond Reservation, the species recorded by Walcott could mostly still be observed in 2008–2012. In fact, the records for 2008–2012 contain many more species than Walcott observed, but we do not know whether this is because of changes in the bird community or a higher sampling intensity in 2008–2012. The life history traits and the species richness at the park-like University of California campus have not changed from 1913–2007, even though the

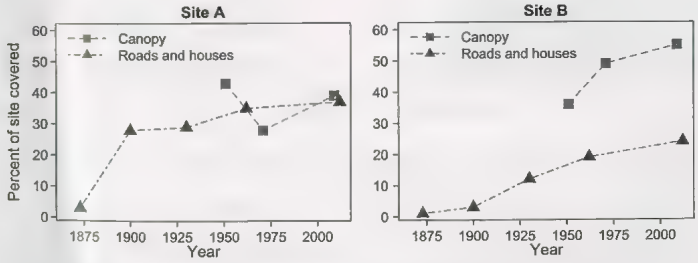


FIG. 4. Changes in housing and road cover between 1872–2012, and tree cover between 1951–2010 at the two residential study sites in Cambridge, Massachusetts.

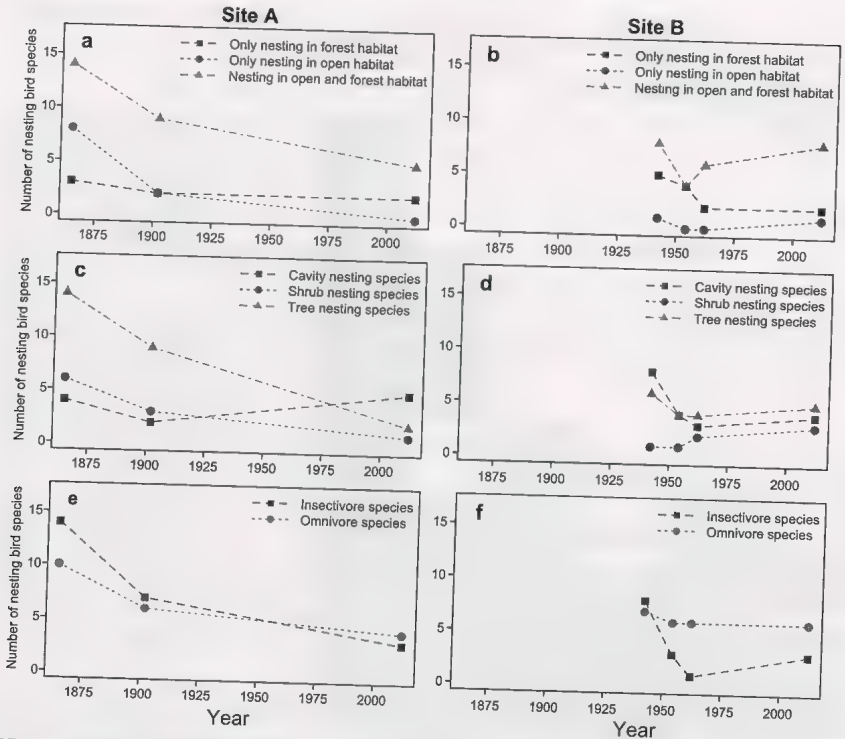


FIG. 5. Life history traits of the nesting bird species at the residential sites A (a, c, e) and B (b, d, f). Panel a and b show habitat preferences, c and d show nesting preferences, and e and f food preferences.

community composition has changed significantly (Shultz et al. 2012). Batten (1972) also reports high turnover rates for a survey area north of London, UK, between 1830–1970.

At the residential sites in Cambridge, the data suggest clear shifts in community composition rather than just stochastic turnover (i.e., random loss and gain of species, independent of guild) (Table 1; Fig. 5). These shifts and the slight increase in nesting bird species on Site B, despite continuing development since the 1960s, call for a closer look. We discuss several factors that could explain the observed changes.

Habitat Loss and Habitat Change.—The landscapes of New England, as in many other parts of the world, have undergone tremendous changes over the past centuries. When the American writer Henry David Thoreau built his cabin near Walden Pond in eastern Massachusetts in 1854, he reflected on the transformations that had occurred since European settlement, and on the new transitions that were just beginning (Cronon 2011). The forests that once covered New England had largely been cleared for agricultural land and most people lived in rural areas in the middle of the 19th century. However, during that time, the landscape of New England was starting to be transformed again by two driving factors. First, as farmers left for more productive areas that had recently been opened up in the Midwest, farmland was being abandoned, and forests started to re-grow (Hall et al. 2003). The second process that transformed the region was industrialization and the urbanization that came with it (Foster 2001).

The changes in the landscape around Brewster's house in the 19th century mirror those happening in New England at the same time. The open agricultural landscape that still surrounded Site A in the 1860s was well reflected in the bird

TABLE 2. Bird species observed (black) in 1940–1944 and 1960–1964 by Walcott (1974) at Fresh Pond Reservation (66 ha). 2008–2012 records were obtained from eBird (2013) for the months June and July. Transient and nesting species are not differentiated.

Species	1940–44	1960–64	2008–12
Anas rubripes (American Black Duck)	■		
Anas platyrhynchos (Mallard)		■	■
Phasianus colchicus (Ring-necked Pheasant)	■	■	
Butorides virescens (Green Heron)		■	■
Charadrius vociferus (Killdeer)	■		
Actitis macularius (Spotted Sandpiper)	■		
Larus argentatus (Herring Gull)	■	■	■
Chaetura pelagica (Chimney Swift)	■	■	■
Colaptes auratus (Northern Flicker)	■	■	■
Tyrannus tyrannus (Eastern Kingbird)	■	■	■
Vireo gilvus (Warbling Vireo)	■	■	■
Vireo olivaceus (Red-eyed Vireo)	■	■	■
Cyanocitta cristata (Blue Jay)	■	■	■
Corvus brachyrhynchos (American Crow)	■	■	■
Tachycineta bicolor (Tree Swallow)	■		■
Turdus migratorius (American Robin)	■	■	■
Dumetella carolinensis (Gray Catbird)	■	■	■
Toxostoma rufum (Brown Thrasher)		■	■
Sturnus vulgaris (European Starling)	■	■	■
Setophaga petechia (Yellow Warbler)	■	■	■
Geothlypis trichas (Common Yellowthroat)		■	■
Spizella passerina (Chipping Sparrow)	■	■	■
Melospiza melodia (Song Sparrow)	■	■	■
Pheucticus ludovicianus (Rose-breasted Grosbeak)		■	■
Passerina cyanea (Indigo Bunting)		■	
Agelaius phoeniceus (Red-winged Blackbird)	■	■	■
Sturnella magna (Eastern Meadowlark)	■	■	
Quiscalus quiscula (Common Grackle)	■	■	■
Icterus galbula (Baltimore Oriole)	■	■	■
Passer domesticus (House Sparrow)	■	■	■
# Additional species:			33

community. The presence of many species, like Eastern Bluebird (*Sialia sialis*), Eastern Kingbird (*Tyrannus tyrannus*), Bobolink (*Dolichonyx oryzivorus*), or Indigo Bunting (*Passerina cyanea*), was facilitated by open habitat created from agriculture and land clearing (DeGraaf and Yamasaki 2001). The decline of these species may be equally linked to widespread abandonment of farmland during that time and the related habitat change (Foster and Motzkin 2003), as much as to direct habitat loss through urbanization. Likewise, some farmland species have disappeared from a survey area near London, even as pressure from urbanization was still low

(Batten 1972), which can probably be linked to changing agricultural practices during that time (Shrubb 2003).

Just as forest cover in New England recovered in the late 19th and early 20th century (cf., Hall et al. 2003), urbanization in Cambridge was accompanied by an increase in tree cover (Brewster 1906). While Brewster did not find any typical woodland species in 1900–1904, by 1940–1943 the number of species nesting only in forest habitat and the number of cavity nesters peaked (Figs. 5b,d). Forest species like Downy Woodpecker (*Picoides pubescens*), Black-capped Chickadee, and White-breasted Nuthatch were present from 1940–1943 onward. The breeding of the Wood Thrush (*Hylocichla mustelina*) in 1940–1943 and 1953–1955, a forest bird known to nest in semi-wooded residential areas, also suggests that tree cover must have been sufficient by that time. The species became transient in 1960–1964 and was not recorded in 2012, suggesting that overall canopy in the areas surrounding sites A and B could have decreased to a threshold below which Wood Thrushes could not persist. However, the bird can still be found during the breeding season at Mt Auburn Cemetery, ca. 1 km southwest of Site A, according to records on eBird in 2013. Likewise, comparing three suburban bird communities, DeGraaf and Wentworth (1986) found that a 70-year-old development with mature trees had higher species richness than a 15-year-old development with young trees.

There is other evidence that urban trees may have compensated for some of the negative effects of urbanization. Site B has seen slow but continuous development since the 1960s, but the number of species has increased slightly. This could be because of the increase in tree canopy (Fig. 4). Canopy cover, tree height and tree age have been shown to be important factors influencing bird diversity in other cities (DeGraaf and Wentworth 1986, White et al. 2005, MacGregor-Fors 2008).

Another land-use/land-cover change that that probably contributed to the bird community changes was the loss of wetlands and open water in the wider surroundings of the sites. A map of the area in 1866 shows a reservoir and a maple swamp within just 500 m of sites A and B (plate 7 in Brewster 1906). The reservoir was filled and developed around 1900, and the wetlands in the area disappeared with continuing urbanization (Howard 1974, Sinclair 2009). This probably had a major impact on food resource availability for insectivore species. Tree Swallows (*Tachycineta bicolor*) in particular utilize wetlands and ponds in the vicinity of their nests (St Louis et al. 1990, Winkler et al. 2011). By 1900 they were absent from Site A. Tree Swallows are nesting today at Fresh Pond Reservation (Hrycyna 2013), but they were recorded as transients in 1940–1944 (Walcott 1974; Table 2). Unfortunately, we have no information on when they returned. Similarly, Warbling Vireo (*Vireo gilvus*) and Yellow Warbler (*Setophaga petechia*) are documented nesting at Fresh Pond from 1940 until today (Walcott 1974, Hrycyna 2013). Both are insectivores that tend to nest near water (Lowther et al. 1999, Gardali and Ballard 2000), and both were last observed nesting on Site A in 1860–1873 and 1900–1904, respectively.

Even seemingly small changes within already urbanized areas can affect the bird community. The presence of the Common Nighthawk (*Chordeiles minor*) as a transient at Site B between 1940 and 1964 may be linked to a certain kind of gravel roof cover that became popular during that time (Walcott 1953). Since then, such roofs have come out of favor, which is believed to be one reason for the declining numbers of the species (Brigham et al. 2011).

Invasive Species.—Brewster (1906), Townsend (1920), and Walcott (1974) recall the introduction of House Sparrows and European Starlings as having a devastating effect on the local native bird community. The authors mainly attribute this to competition for nesting space. However, there is little evidence that invasive species as a single factor have caused local extinctions (Koenig 2003, Gurevitch and Padilla 2004). Some of the species that Brewster (1906) deemed to be most threatened by House Sparrows, like Tree Swallow and Song Sparrow, are still nesting at nearby Fresh Pond today and have more likely disappeared from residential sites because of habitat change. It is interesting to note that Tree Swallows at Fresh Pond Reservation were mainly nesting in nest boxes in 2012 (Hrycyna 2013). However, without a detailed investigation, it is not possible to attribute their nest site selection to competition with House Sparrows or other species versus a simple lack of natural cavities (tree snags, etc.) in this highly managed park.

One species that is widely believed to have been affected and locally replaced by the invasive

House Finch is the Purple Finch (*Haemorhous purpureus*) (Wootton 1987, 1996). Purple Finches have been nesting or transient for most survey periods between 1860–1964, but they can no longer be found in Cambridge during the breeding season (Mass Audubon 2013). House Finches arrived in the region in the 1960s (Badyaev et al. 2012) and are nesting on Site B today. This effect is widely assumed to be the result of habitat and resource competition (Wootton 1987, 1996).

Pesticide Spraying.—Invasive species of a different kind had severe indirect effects on birds in much of the 20th century. Around 1868, the Gypsy Moth was accidentally released very close to the study sites, in Medford, Massachusetts (Liebhold et al. 1992). Efforts to eradicate the tree pest were quickly under way, and Walcott (1974) reports that lead arsenate shade tree spraying began in 1912. In the 1930s, devastating Dutch Elm disease started spreading in the Northeast, and again pesticides were used as means to control elm bark beetles, which are vectors of the disease (Wallace et al. 1961). DDT and Sevin replaced lead arsenate in the 1940s and 1950s (Howard 1974, Walcott 1974). The impacts on local bird populations were quite severe, whether directly or indirectly via impacts on arthropod prey (Townsend 1920, Howard 1974, Walcott 1974).

The decline of the number of nesting pairs of American Robins at the sites in Cambridge could be an indicator of the negative impacts of pesticide spraying. Numbers declined from 5–8 pairs in the 1860s to just one in 1960–1964 (Walcott 1974). However, it is not clear whether pesticides singularly caused the local extinction of insectivores or whether pesticides enhanced stress induced by ongoing habitat change. For example, between 1873–1900, insectivores declined more strongly than omnivores despite the absence of pesticide spraying (Fig. 5e).

When exactly tree spraying stopped in Cambridge could not be determined, but it has not been practiced for at least two decades (K. Writer, Cambridge Parks and Forestry Division within the Dept. of Public Works, pers. comm.). In some years, pesticides are still applied against vectors of human diseases, like West Nile virus, but this has only happened once or twice since 1982 at the study sites (D. Henley, East Middlesex Mosquito Control Project, pers. comm.). The environment in Cambridge is probably much less toxic with regard to pesticides today than when birds were last studied in the 1960s. This could be a cause for the slight increase in insectivore species on Site B (Fig. 5f) and the much higher population of American Robins (on average, 10 individuals were encountered at Site B on each surveying day in 2012).

Range Expansions.—Several species have expanded their range in the 20th century and are new to the bird community of Cambridge today: Northern Cardinal (*Cardinalis cardinalis*), Tufted Titmouse (*Baeolophus bicolor*), Northern Mockingbird (*Mimus polyglottos*), Carolina Wren, and Mourning Dove. In fact, some of the increase in nesting bird species on Site B between 1964 and today is because of species that have expanded their geographic range (Table 1). These range expansions have probably been facilitated by several factors, namely habitat change, climate change, and foraging resources (Beddall 1963). Supplementary feeding and exotic vegetation of cities have been shown to be of particular importance for some species, thereby shifting dominance patterns in urban bird communities (Rodewald and Shustack 2008, Ortega-Álvarez and MacGregor-Fors 2009, Shochat et al. 2010). Bird feeders were frequently encountered at sites A and B in 2012, and Walcott reports in 1953 that "more people than ever before are feeding wild birds."

Conclusions.—The 150 years of bird data from Cambridge tell a compelling story about dynamics of change in bird communities in human-dominated habitats. When our time series is viewed as a rural-urban gradient, the general patterns found in recent "space-for-time" substitution studies emerge (cf., Chace and Walsh 2006, Devictor et al. 2006, Tratalos et al. 2007, Shanahan et al. 2014). Adding time as a dimension reveals a multitude of additional factors that "urbanization" in Cambridge has encompassed: land cover change from open agricultural land to urban and wooded habitats; loss and re-growth of tree canopy; introductions of new species or species that have expanded their ranges; and widespread use of pesticides.

The rich farmland bird community that Brewster observed around his home in the 19th century had fundamentally changed by the mid-20th century. To Walcott, the new bird community seemed unattractive as compared to the one that was lost (Walcott 1959). We see the changes from a broadened perspective. The reappearances of forest species such as Black-capped Chickadee

and White-breasted Nuthatch, which were absent from these Cambridge neighborhoods in Brewster's time, illustrate a wider (if unplanned) ecological success story—the reforestation of the eastern United States since 1850. In fact, it can be argued that some species that disappeared locally in Cambridge in the 20th century were present in the 19th century only because of massive disruption to the preexisting forested landscape of New England.

Evidence from the reported time series highlights that choices we make in urban environments can have positive as well as negative effects on bird populations. Most bird species disappeared during periods after major building developments and in that respect, the recent trend of re-urbanization and densification of Cambridge and other cities has to be carefully monitored and mitigated. Planting of trees and ending pesticide spraying seem to have contributed to stabilizing or even increasing populations of several bird species in Cambridge. Parks like Fresh Pond Reservation serve as local refuges for species that do not thrive in nearby residential neighborhoods. These park spaces may take on increased conservation significance as urbanization increases (Shultz et al. 2012, Shanahan et al. 2014). The patterns revealed in this analysis of 150 years of changes in bird life in Cambridge provide further support for urban planning guidelines for preservation of large urban green space and retention of higher densities of mature urban trees in residential areas.

ACKNOWLEDGMENTS

We thank the residents of sites A and B, who have been extremely welcoming and enthusiastic about our study. We also thank V. Wolff and the Urban Ecology Institute for help with contacting residents, J. Amero from the city of Cambridge IT Department for providing GIS data, and the anonymous reviewers for their comments. Support for this study came from Massachusetts Agricultural Experiment Station and the Department of Environmental Conservation under Project No. MAS009584, paper number 3468 and the National Science Foundation under Grant No. BCS-0948984. Any opinions, findings and conclusions or recommendation expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation (NSF).

LITERATURE CITED

ATLAS OF THE CITY OF CAMBRIDGE MASSACHUSETTS. 1930. G. W. Bromley and Co., Philadelphia, USA.

BADYAEV, A. V., V. BELLONI, AND G. E. HILL. 2012. House Finch (*Haemorhous mexicanus*). The birds of North America. Number 46.

BATTEN, L. A. 1972. Breeding bird species diversity in relation to increasing urbanisation. Bird Study 19:157–166.

BEDDALL, B. G. 1963. Range expansion of the cardinal and other birds in the northeastern states. Wilson Bulletin 75:140–158.

BREWSTER, W. 1906. The birds of the Cambridge region of Massachusetts. Memoirs of the Nuttall Ornithological Club, Cambridge, Massachusetts, USA.

BRIGHAM, R. M., J. NG, R. G. POULIN, AND S. D. GRINDAL. 2011. Common Nighthawk (*Chordeiles minor*). The birds of North America. Number 213.

BROMLEY, G. W. AND W. S. BROMLEY. 1916. Atlas of the city of Cambridge, Massachusetts. G. W. Bromley and Co., Philadelphia, USA.

BUTCHER, G. S., M. R. FULLER, L. S. MCALLISTER, AND P. H. GEISSLER. 1990. An evaluation of the Christmas Bird Count for monitoring population trends of selected species. Wildlife Society Bulletin 18:129–134.

CAMBRIDGE HISTORICAL COMMISSION. 2012. A brief history of Cambridge, Massachusetts, USA. City of Cambridge. www2.cambridgema.gov/Historic/cambridgehistory.html (accessed 2 May 2013).

CHACE, J. F. AND J. J. WALSH. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46–69.

COLWELL, R. K., C. X. MAO, AND J. CHANG. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717–2727.

COMMONWEALTH OF MASSACHUSETTS. 2012. Office of Geographic Information (MassGIS). www.mass.gov/mgis/massgis.htm (accessed 2 May 2013).

CRONON, W. 2011. Changes in the land. Hill and Wang, New York, USA.

DAUGHTERS OF THE AMERICAN REVOLUTION. 1907. An historic guide to Cambridge. Hannah Winthrop Chapter, N.S.D.A.R., Cambridge, Massachusetts, USA.

DAVIS, A. M. AND T. F. GLICK. 1978. Urban ecosystems and island biogeography. Environmental Conservation 5:299–304.

DEGRAAF, R. M. AND J. M. WENTWORTH. 1986. Avian guild structure and habitat associations in suburban bird communities. Urban Ecology 9:399–412.

DEGRAAF, R. M. AND M. YAMASAKI. 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Lebanon, USA.

DEVICTOR, V., R. JULLIARD, D. COUVET, A. LEE, AND F. JIGUET. 2006. Functional homogenization effect of urbanization on bird communities. Conservation Biology 21:741–751.

EBIRD. 2013. eBird: An online database of bird distribution and abundance. eBird, Ithaca, New York. www.ebird.org (accessed 27 Nov 2013).

ESRI WORLD TOPOGRAPHIC MAP SERVICE. 2012. Esri, DeLorme, NAVTEQ, TomTom, Intermap, iPC,

USGS, FAO, NPS, NRCAN, GeoBase, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), and the GIS User Community.

Evans, K. L., B. J. Hatchwell, M. Parnell, and K. J. Gaston. 2010. A conceptual framework for the colonisation of urban areas: the blackbird *Turdus merula* as a case study. Biological Reviews 85:643–667.

Foster, D. R. 2001. Thoreau's Country. Harvard University Press, Cambridge, Massachusetts, USA.

Foster, D. R. and G. Motzkin. 2003. Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. Forest Ecology and Management 185:127–150.

Fry, D. M. 1995. Reproductive effects in birds exposed to pesticides and industrial chemicals. Environmental Health Perspectives 103:165–171.

Gardali, T. and G. Ballard. 2000. Warbling Vireo (*Vireo gilvus*). The birds of North America. Number 551.

Gibson, C. 1998. Population of the 100 largest cities and other urban places in the United States: 1790 to 1990. U.S. Bureau of the Census Population Division, Washington, D.C. www.census.gov/population/www/documentation/twps0027.html (accessed 2 May 2013).

Gurevitch, J. and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology and Evolution 19:470–474.

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2003. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography 29:1319–1335.

Hopkins, G. M. 1873. Atlas of the city of Cambridge, Middlesex Co., Massachusetts. G. M. Hopkins & Co., Philadelphia, USA.

Howard, D. V. 1974. Urban robins: a population study. Pages 67–75 *in* A symposium on wildlife in an urbanizing environment, November 27–29, 1973, Springfield Massachusetts (J. H. Noyes and D. R. Progulske, Editors). Cooperative Extension Service, University of Massachusetts, Amherst, USA.

Hrycyna, A. 2013. Exploring the world through Black's Nook: an experiment in collaborative patch birding in Cambridge, Massachusetts. Bird Observer 41:160–165.

Insurance Maps of Cambridge Massachusetts. 1900. Sandborn-Perris Map Co.

Insurance Maps of Cambridge Massachusetts. 1962. Sandborn-Perris Map Co.

Koenig, W. D. 2003. European Starlings and their effect on native cavity-nesting birds. Conservation Biology 17:1134–1140.

Liebhold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. Journal of Biogeography 19:513–520.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimner, and D. A. Spector. 1999. Yellow Warbler (*Dendroica petechia*). The birds of North America. Number 45.

MacGregor-Fors, I. 2008. Relation between habitat attributes and bird richness in a western Mexico suburb. Landscape and Urban Planning 84:92–98.

Major, R. E. and H. Parsons. 2010. What do museum specimens tell us about the impact of urbanisation? A comparison of the recent and historical bird communities of Sydney. Emu 110:92–103.

Marzluff, J., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms, and approaches. Pages 1–17 *in* Avian ecology and conservation in an urbanizing world (J. Marzluff, R. Bowman and R. Donnelly, Editors). Springer, New York, USA.

Mass Audubon. 2008. Handbook for the Massachusetts Breeding Bird Atlas 2. www.massaudubon.org/content/download/8933/152595/file/handbook.pdf (accessed 13 Dec 2013).

Mass Audubon. 2013. Breeding Bird Atlas 2 Species Accounts, Purple Finch. www.massaudubon.org/our-conservation-work/wildlife-research-conservation/statewide-bird-monitoring/breeding-bird-atlases/bba2/find-a-bird/(id)/6212 (accessed 13 Dec 2013).

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and Helene Wagner. 2011. Vegan: community ecology package version 2.0-9. CRAN.R-project.org/package=vegan (accessed 22 Nov 2013).

O'Neil-Dunne, J. 2012. A report on the city of Cambridge's existing and possible tree canopy. unpublished.

Ortega-Álvarez, R. and I. MacGregor-Fors. 2009. Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. Landscape and Urban Planning 90:189–195.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. G. Boone, P. M. Groffman, E. Irwin, S. S. Kaushal, V. Marshall, B. P. McGrath, C. H. Nilon, R. V. Pouyat, K. Szlavecz, A. Troy, and P. Warren. 2011. Urban ecological systems: scientific foundations and a decade of progress. Journal of Environmental Management 92:331–362.

Rodewald, A. D. and D. P. Shustack. 2008. Consumer resource matching in urbanizing landscapes: are synanthropic species over-matching. Ecology 89: 515–521.

Shanahan, D. F., M. W. Strohbach, P. S. Warren, and R. A. Fuller. 2014. The challenges of urban living. Pages 3–20 *in* Avian Urban Ecology (D. Gil and H. Brumm, Editors). Oxford University Press, Oxford, UK.

Shochat, E., S. B. Lerman, J. M. Anderies, P. S. Warren, S. H. Faeth, and C. H. Nilon. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60:199–208.

Shrubb, M. 2003. Birds, scythes, and combines: a history of birds and agricultural change. Cambridge University Press, Cambridge, UK.

Shultz, A. J., M. W. Tingley, and R. C. K. Bowie. 2012. A century of avian community turnover in an urban green space in northern California. Condor 114:258–267.

Sinclair, J. 2009. Fresh Pond: the history of a Cambridge landscape. MIT Press, Cambridge, Massachusetts, USA.

ST LOUIS, V. L., L. BREEBAART, AND J. C. BARLOW. 1990. Foraging behaviour of Tree Swallows over acidified and nonacidic lakes. Canadian Journal of Zoology 68:2385–2392.

TOWNSEND, C. W. 1920. Supplement to the birds of Essex County, Massachusetts. Memoirs of the Nuttall Ornithological Club, Cambridge, Massachusetts, USA.

TRATALOS, J., R. A. FULLER, K. L. EVANS, R. G. DAVIES, S. E. NEWSON, J. J. D. GREENWOOD, AND K. J. GASTON. 2007. Bird densities are associated with household densities. Global Change Biology 13:1685–1695.

U.S. CENSUS BUREAU. 2012. Cambridge, Massachusetts. quickfacts.census.gov/qfd/states/25/2511000.html (accessed 2 May 2013).

WALCOTT, C. F. 1953. Some trends in city bird life from 1870 to 1940. Bulletin of the Massachusetts Audubon Society 37:187–189.

WALCOTT, C. F. 1959. Effects of city growth on bird life. Massachusetts Audubon 43:120–122.

WALCOTT, C. F. 1974. Changes in bird life in Cambridge, Massachusetts from 1860 to 1964. Auk 91:151–160.

WALLACE, G. J., W. P. NICKELL, AND R. F. BERNARD. 1961. Bird mortality in the Dutch Elm disease program in Michigan. Cranbrook Institute of Science, Bloomfield Hills, Michigan, USA.

WHITE, J., M. ANTOS, J. FITZSIMONS, AND G. PALMER. 2005. Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. Landscape and Urban Planning 71:123–135.

WINKLER, D. W., K. K. HALLINGER, D. R. ARDIA, R. J. ROBERTSON, B. J. STUTCHBURY, AND R. R. COHEN. 2011. Tree Swallow (*Tachycineta bicolor*). The birds of North America. Number 11.

WOOTTON, J. T. 1987. Interspecific competition between introduced House Finch populations and two associated passerine species. Oecologia 71:325–331.

WOOTTON, J. T. 1996. Purple Finch (*Haemorhous purpureus*). The birds of North America. Number 208.

The Wilson Journal of Ornithology 126(2):207–217, 2014

THE HISTORICAL DISTRIBUTION OF GUNNISON SAGE-GROUSE IN COLORADO

CLAIT E. BRAUN,[1,7] SARA J. OYLER-MCCANCE,[2] JENNIFER A. NEHRING,[3] MICHELLE L. COMMONS,[4] JESSICA R. YOUNG,[5] AND KIM M. POTTER[6]

ABSTRACT.—The historical distribution of Gunnison Sage-Grouse (*Centrocercus minimus*) in Colorado is described based on published literature, observations, museum specimens, and the known distribution of sagebrush (*Artemisia* spp.). Historically, Gunnison Sage-Grouse were widely but patchily distributed in up to 22 counties in south central and southwestern Colorado. The historical distribution of this species was south of the Colorado-Eagle river drainages primarily west of the Continental Divide. Potential contact areas with Greater Sage-Grouse (*C. urophasianus*) were along the Colorado-Eagle river system in Mesa, Garfield, and Eagle counties, west of the Continental Divide. Gunnison Sage-Grouse historically occupied habitats that were naturally highly fragmented by forested mountains and plateaus/mesas, intermountain basins without robust species of sagebrush, and river systems. This species adapted to use areas with more deciduous shrubs (i.e., *Quercus* spp., *Amelanchier* spp., *Prunus* spp.) in conjunction with sagebrush. Most areas historically occupied were small, linear, and patchily distributed within the overall landscape matrix. The exception was the large intermountain basin in Gunnison, Hinsdale, and Saguache counties. The documented distribution east of the Continental Divide within the large expanse of the San Luis Valley (Alamosa, Conejos, Costilla, and Rio Grande counties) was minimal and mostly on the eastern, northern, and southern fringes. Many formerly occupied habitat patches were vacant by the mid 1940s with extirpations continuing to the late 1990s. Counties from which populations were recently extirpated include Archuleta and Pitkin (1960s), and Eagle, Garfield, Montezuma, and Ouray (1990s). *Received 1 November 2013. Accepted 29 January 2014.*

Key words: *Centrocercus minimus*, *C. urophasianus*, Colorado, Greater Sage-Grouse, Gunnison Sage-Grouse.

The Gunnison Sage-Grouse (*Centrocercus minimus*) was not described as a species separate from Greater Sage-Grouse (*C. urophasianus*) until 2000 (Young et al. 2000). They were known to differ from Greater Sage-Grouse by 1977 and were subsequently investigated in a series of studies starting in the mid 1980s (Hupp 1987) and 1990s (Young 1994, Commons 1997, Oyler-McCance 1999). These studies characterized many different aspects including morphology (Hupp and Braun 1991), behavior (Young et al. 1994), habitat (Commons et al. 1999, Oyler-McCance et al. 2001), and genetics (Oyler-McCance et al. 1999).

The distribution of sage-grouse in North America, including Gunnison Sage-Grouse, was most recently reported by Schroeder et al. (2004) while Rogers (1964) and Braun (1995) described the early distribution of sage-grouse in Colorado. Young et al. (2000) described the general historical and current distribution of Gunnison Sage-Grouse when they formally described the species. This information is particularly important as Gunnison Sage-Grouse populations have declined dramatically (Gunnison Sage-Grouse Rangewide Steering Committee 2005) and the species has been proposed for listing as endangered under the U.S. Endangered Species Act (USDI 2013).

The oldest fossil evidence of sage-grouse (Emslie 2004) suggests they existed in Colorado in the early Pleistocene (~1.6 million years ago). Anecdotal accounts of sage-grouse in Colorado are available (Morrison 1888, Cooke 1897, Rockwell 1908, Warren 1909, Sclater 1912, Bergtold 1928) and provide some evidence of where sage-grouse occurred in the late 1800s and early 1900s. Additionally, Rogers (1964) summarized the distribution of sage-grouse and sagebrush (*Artemisia* spp.) in Colorado in the late 1950s and early 1960s. These accounts provide important information on the historical distribution of Gunnison Sage-Grouse. Additional information exists in the form of museum specimens, personal communications with ranchers and wildlife managers, and field work specifically searching for evidence of sage-grouse that can be used to refine the

[1] Grouse Inc., Tucson, AZ 85750, USA.
[2] U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Fort Collins, CO 80526, USA.
[3] Wetland Dynamics, LLC., 3393 E County Road, 9 S, Monte Vista, CO 81144, USA.
[4] Idaho Department of Fish and Game, Nampa, ID 83686, USA.
[5] Western State Colorado University, 600 North Adams Street, Gunnison, CO 81231, USA.
[6] USDA Forest Service, 94 County Road, 244, Rifle, CO 81650, USA.
[7] Corresponding author; e-mail: sgwtp66@gmail.com

historical distribution of Gunnison Sage-Grouse in Colorado. The objectives of this study were to (1) review all pertinent information regarding Gunnison Sage-Grouse to define the historical distribution in Colorado, and (2) provide the timing of recent population extirpations.

METHODS

We reviewed the early published literature on avifauna (and sage-grouse) in Colorado, attempted to locate specimens in museums by circulating requests in the ornithological literature, and interviewed people who lived and or worked in areas depicted as historical range by Rogers (1964:fig. 1). We also examined historic journals describing some of the first documented reports of flora and fauna in areas possibly occupied by Gunnison Sage-Grouse in the 1800s. Of particular use was the Beckwith (1855) account of Captain Gunnison's explorations (1853–1854) in New Mexico and Colorado, as well as the Coues (1898) account of Major Fowler's 1821–1822 journey through several western states including Oklahoma, New Mexico, and Colorado.

We conducted field surveys in spring from 1978 as time permitted to spring 1999 in areas reported by Rogers (1964) to have had sage-grouse. We restricted our investigations to areas generally south of the Colorado River from the Colorado-Utah State line east to the junction with the Eagle River and from there east to the Continental Divide. We included all sagebrush habitats south of Interstate 70 east of the Continental Divide (especially in Lake, Park, and Chaffee counties), and all areas within the San Luis Valley to the Colorado-New Mexico State line and west to the Arizona-Utah State boundaries. This included all of southwest Colorado and immediately adjacent counties within Colorado. We also surveyed and viewed sage-grouse in all counties (Mesa, Garfield, and Eagle) immediately north of the Colorado-Eagle rivers. We selected this area as all sage-grouse north of the Colorado-Eagle rivers were known to be Greater Sage-Grouse (Hupp and Braun 1991). These areas were open (except Mesa County) to hunting of sage-grouse and data (observations and wing collections) were available precluding the presence of Gunnison Sage-Grouse.

RESULTS

The oldest fossil evidence of sage-grouse is from the early Pleistocene (~1.6 million years ago) in central Colorado (i.e., Park County, 20 km northeast of present Salida in Chaffee County) (Emslie 2004). This is ~35 km northeast of the present population of Gunnison Sage-Grouse at Poncha Pass in Saguache County. Early reports of sage-grouse distribution in Colorado include Cooke (1897), Sclater (1912), and Bergtold (1928). Cooke (1897:71) reported that sage-grouse were common residents in Colorado with a few ranging to 2,896 m in summer and were much more common in the northern half of the state. Sclater (1912) reported the presence of sage-grouse in Gunnison and Mesa counties, near Cortez in Montezuma County, and in the lower Trinchera Valley in Costilla County. Bergtold (1928:97) reported sage-grouse were frequent residents occurring locally in more northern parts of Colorado up to 2,743 m in elevation. Rogers (1964) reported sage-grouse occurred in the southwestern Colorado counties of Archuleta, Delta, Dolores, Eagle, Garfield, Gunnison, La Plata, Mesa, Montezuma, Montrose, Ouray, Pitkin, Saguache, and San Miguel. He also suggested (1964:9) the eastern slope counties of Alamosa, Chaffee, Lake, Conejos, Costilla, Rio Grande, and possibly Huerfano likely contained sage-grouse.

Rogers (1964:fig. 3) reported on the distribution of sagebrush which was present in southwestern Colorado at Iron Springs Divide, Uncompahgre Plateau, Plateau Creek, Roaring Fork Valley to Aspen, Lone Cone, Lone Mesa, Naturita, Cerro Ridge, Somerset, Marshall Pass, Durango, Crested Butte, Sapinero, Gunnison, Creede, Poncha Pass, Buena Vista, Leadville, Hotchkiss, Saguache, Bayfield, Arboles, and McElmo. Anderson (1969) reported that sagebrush spraying on the Uncompahgre Plateau resulted in loss (emigration) of the sage-grouse from the area. J. D. Hart of the Colorado Game and Fish Department (memo of 1 July 1937 cited in Rogers [1964:20]), reported slight increases in sage-grouse in Archuleta, Dolores, Garfield, Hinsdale, La Plata, Mesa, Montezuma, and Montrose counties during 1936–1937. Hart also reported that populations were static in Delta, Eagle, Gunnison, Mineral, and Saguache counties. While sage-grouse populations in some counties had disappeared by 1944 (Rogers 1964:25), the species was present in Delta, Dolores, Eagle, Garfield, Gunnison, Hinsdale, Mesa, Montezuma, Montrose, Ouray, Saguache, and San Miguel counties in 1961 (Rogers 1964:fig. 9).

TABLE 1. Gunnison Sage-Grouse occurrence in Colorado.

County	Historic occurrence[a]	Where	Current occurrence	When extirpated
Alamosa	Yes	Unknown	No	<1942
Archuleta	Yes	Multiple Areas	No	1960s
Chaffee	Yes	Unknown	No	1940s
Conejos	Yes	Unknown	No	1940s
Costilla	Yes	Trinchera Valley	No	1930s
Delta	Yes	Multiple Areas	Yes	
Dolores	Yes	Multiple Areas	Yes	
Eagle	Yes	Multiple Areas	No	By 1998
Garfield	Yes	Multiple Areas	No	By 1996
Gunnison	Yes	Multiple Areas	Yes	
Hinsdale	Yes	Multiple Areas	Yes	
Huerfano	??	Unknown	No	<1930?
La Plata	Yes	Multiple Areas	No	<1960
Mesa	Yes	Multiple Areas	Yes	
Mineral	Yes	Unknown	No	<1940
Montezuma	Yes	Multiple Areas	No	By 1996
Montrose	Yes	Multiple Areas	Yes	
Ouray	Yes	Multiple Areas	No	By 1996
Pitkin	Yes	Multiple Areas	No	By 1965
Rio Grande	Yes	Unknown	No	<1940
Saguache	Yes	Multiple Areas	Yes	
San Miguel	Yes	Multiple Areas	Yes	

[a] Based on Rogers 1964.

Based on a review of the literature, personal communications with ranchers and wildlife managers, museum specimens (27 from Dolores [1], Gunnison [11], Mesa [1], Montrose [1], Saguache [6], and San Miguel [7] counties), and actual searches for birds, the historical distribution of Gunnison Sage-Grouse in Colorado (Table 1, Fig. 1) was as described below.

Alamosa, Conejos, Costilla, and Rio Grande Counties.—Captain J. W. Gunnison reported "grouse" (species not identified) in his 1853 expedition through the Sangre de Cristo Mountains and San Luis Valley of Colorado (Beckwith 1855). He arrived in the San Luis Valley from Huerfano County (to the east), over the Sangre de Cristo Mountains and then proceeded south to Taos, New Mexico, through the south end of the Valley. He returned to Fort Massachusetts (north of present Fort Garland) and proceeded north to Poncha Pass and west into the Gunnison Basin through Saguache County. This travel included at least Alamosa, Costilla, and Saguache counties, the southern portion of Chaffee County, and possibly Conejos and Rio Grande counties. This report commonly mentioned the presence of sagebrush (specifically *Artemisia*) throughout the area and on two occasions and in two different locations grouse are mentioned in the San Luis Valley.

Major Fowler did not mention grouse of any kind during his travels in the San Luis Valley, although he mentioned killing other birds for food (Coues 1898). Sclater (1912) (per Brunner in litt.) reported the presence of sage-grouse in the lower Trinchera Valley of Costilla County. Rogers (1964:20) suggested that sage-grouse persisted in this county into the late 1930s but may have been eliminated by subsistence hunting.

Intensive field investigations (by JRY) in 1989 on the Forbes Trinchera Ranch (~657,277 ha of which ~98,839–123,548 ha appeared to be potential habitat for sage-grouse) in Costilla County revealed no evidence of the presence of sage-grouse. Rogers (1964) reported there was only limited (~16 km^2) sagebrush in Conejos County. We could not document the presence of sage-grouse in Alamosa, Conejos, Costilla, and Rio Grande counties (but see Sclater 1912 for Costilla County), although they are inferred to have been historically present by Rogers (1964:fig. 1). The presence of sage-grouse in these counties was not included on distribution

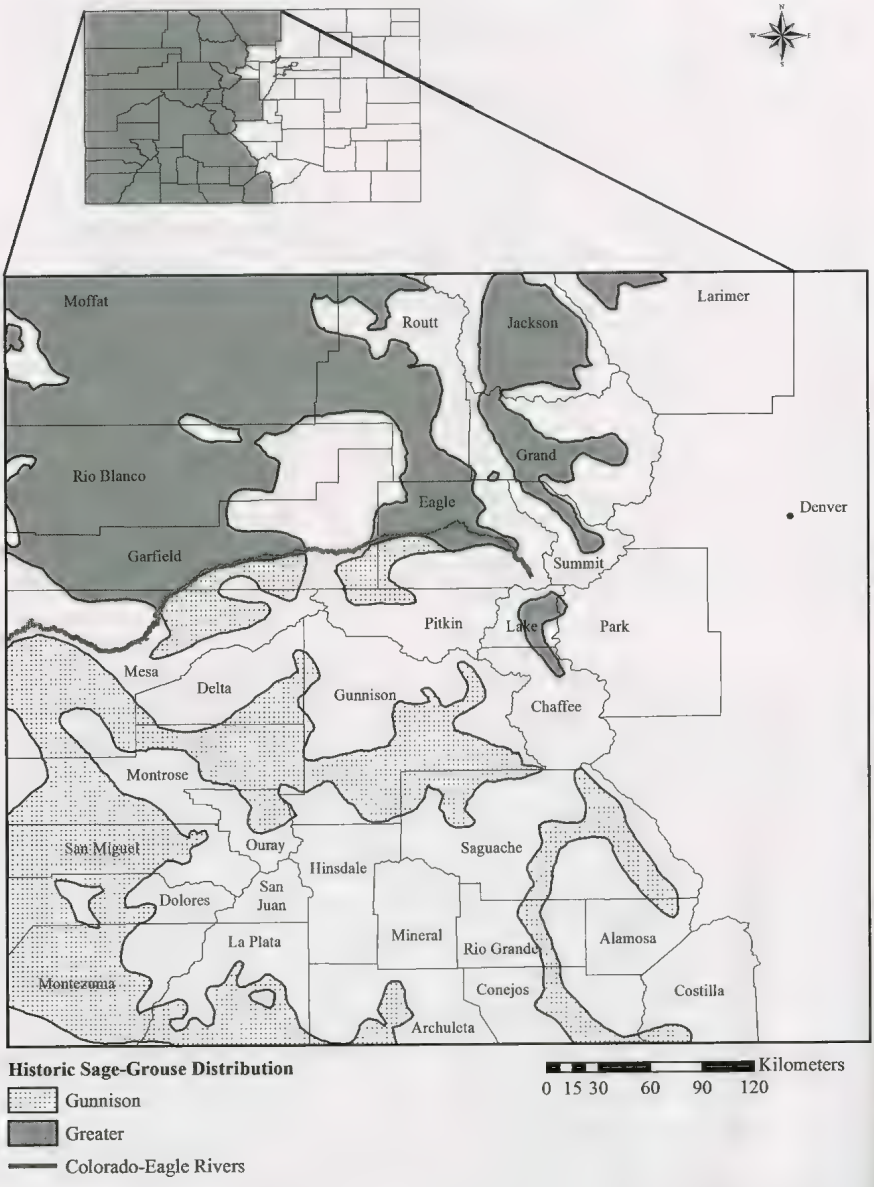


FIG. 1. Assumed historical distribution (1961) of Gunnison Sage-Grouse and Greater Sage-Grouse in Colorado (modified from Rogers 1964).

maps for 1942 or 1945 (Rogers 1964:22–23). These populations were likely extirpated in the late 1930s to early 1940s.

Archuleta County.—Sage-grouse were present in this county in the early 1940s to at least 1945 (Rogers 1964). Pat Waters of the Colorado Game, Fish and Parks Department recalled in the early 1970s that sage-grouse had persisted into the early 1960s near Arboles. This population was probably extirpated as the result of completion and filling of the Navajo Reservoir in 1962.

Chaffee County.—Captain J. W. Gunnison did not report any grouse during his brief travels in 1853 north of Poncha Pass into southern Chaffee County to the Arkansas River (Beckwith 1855). Rogers (1964) suggested that sage-grouse likely occurred in Chaffee County as the sage-grouse hunting season was closed in this county in 1944. The closest historic record is in Park County to the northeast dating to the early Pleistocene (Emslie 2004). The closest current record is about 2 km south of Poncha Pass in Saguache County.

Delta County.—Rogers (1964) indicated sage-grouse were present in the Smith Fork drainage in the southeast part of Delta County and near Dry Fork Creek on the Montrose-Delta County boundary. Gunnison Sage-Grouse were known to persist in the area (Fruitland Mesa) near Crawford during 1978 to the present. Counts of males on leks were made annually during this period and some birds were radiomarked and studied (Commons 1997).

Dolores County.—Bent (1932:309) reported sage-grouse near the town of Dolores. They historically occurred in the western portion of the county with main concentrations northwest of Dolores and a scattered population near Dove Creek and Cahone (Rogers 1964, Bailey and Niedrach 1965). Rogers (1964) reported that sage-grouse hunting was closed in Dolores County in 1960. A flock of 100 sage-grouse was reported in the Groundhog Lake area at the head of Disappointment Creek in 1960. Bill Fischer of the Colorado Game, Fish and Parks Department reported (to the senior author) a flock of 52 sage-grouse on Sage Hen Flats along the Dolores River, on the west edge of Dolores in winter 1976–1977. This area was to be flooded by construction of a new reservoir. He believed these birds summered south of Groundhog Reservoir. Gunnison Sage-Grouse were radiomarked and studied in the mid 1990s northeast and northwest of Dove Creek (Commons 1997).

Eagle County.—Rogers (1964) reported that sage-grouse hunting was closed in Eagle County in 1961. Birds were present south of the Colorado-Eagle rivers in 1961 southwest of Gypsum near the heads of Cattle and Coulter creeks, and near Missouri Heights (Rogers 1964). These birds were known to be small-bodied sage-grouse (P. D. Olson, Colorado Division of Wildlife, pers. obs.). Kevin L. Berner found a hatched sage-grouse nest in early July 1979 along the road (Mayer Gulch) to Hardscrabble Mountain. Tom Verry, working for the Colorado Division of Wildlife, flushed 3 sage-grouse of unknown sex in Mayer Gulch on 20 March 1991 and a hen on 30 April 1991 on Bellyache Ridge. Sage-grouse persisted in this area into the mid to late 1990s, as droppings were found in several locations (southwest of Brush Creek, Bellyache Ridge) in 1995 (CEB, SJO-M, pers. obs.) including near the airport. Displaying sage-grouse were not heard in an intensive search using a parabolic ear in spring 1998 by Wildlife Manager Bill Heicher of the Colorado Division of Wildlife. The population was likely extirpated in the late 1990s.

Garfield County.—Rockwell (1908) reported sage-grouse with young in southern Garfield County near Mamm Creek. Rogers (1964) reported that the hunting of sage-grouse in Garfield County was closed in 1958. Birds were present in 1961 south of the Colorado River (Rogers 1964). Sage-grouse were known to occur in the Cattle and Coulter creek areas near Cottonwood Pass, and also in the Dry Park-Jerome Park area west of the Roaring Fork River and the town of Carbondale (Rogers 1964). T. D. I. Beck of the Colorado Division of Wildlife reported seeing two small active leks each with 5–6 birds south of Glenwood Springs in 1977–1978. Sage-grouse and their droppings were seen near Colorado Mountain College southeast of Glenwood Springs, and Parry A. Larsen reported seeing up to 5 sage-grouse in Spring Valley for 3–5 years prior to 1992. CEB found old droppings at several locations in Spring Valley in 1994. The population was likely extirpated in the mid 1990s.

Gunnison County.—Captain J. W. Gunnison reported sage-grouse in his travels in 1853 near present Elk Creek east of the Lake Fork of the Gunnison River (Beckwith 1855). This report commonly mentioned the presence of sagebrush throughout the area. Sclater (1912) reported the presence of sage-grouse in Gunnison County, as did Warren (1916) who reported sage-grouse were

rare in the Elk Mountain region of Gunnison County and did not occur much farther up the East River than Jack's Cabin. Scattered birds were found elsewhere in this county in sagebrush habitat (Rogers 1964, Bailey and Niedrach 1965). Rogers (1964:20) suggested that Gunnison County historically had some of the highest populations of sage-grouse. This continues, especially in the Ohio Creek and Willow Creek drainages, and Elk Creek (CEB, pers. obs.). This population was intensively studied from the mid 1980s to 1999 (Hupp and Braun 1989; Young et al. 1994, 2000; Oyler McCance et al. 1999, 2001).

Hinsdale County.—Sage-grouse were present in this county in the early 1940s (Rogers 1964) and continue to seasonally occupy habitat in the northern part of the county along upper Powderhorn Creek and the upper Lake Fork of the Gunnison River.

Huerfano County.—Captain J. W. Gunnison passed through Huerfano County in his travels through southern Colorado in 1853 and reported grouse (possibly Dusky Grouse [*Dendragapus obscurus*]) and 'pheasants' (possibly Sharp-tailed Grouse [*Tympanuchus phasianellus*] based on written descriptions in Beckwith 1855) before he crossed the Sangre de Cristo Mountains into the San Luis Valley. Rogers (1964:9) suggested it was possible that sage-grouse once occurred in this county.

La Plata County.—Sage-grouse were present in the early 1940s (Rogers 1964) in this county and occurred along the Pine and Florida rivers, south of Bayfield. Other areas where sage-grouse occurred were south of Hesperus near Breen and Red Mesa. Several older ranchers in these areas mentioned to CEB the past presence of sage-grouse in the pre-1969 interval. This population appears to have been extirpated prior to 1960.

Mesa County.—Rockwell (1908) reported the presence of sage-grouse in Mesa County in March ~12 km south of DeBeque, in summer in Plateau Valley, and in July at the base of Mamm's Peak. Sclater (1912) also reported the presence of sage-grouse in this county. Rogers (1964) observed males displaying in Glade Park and on Pinon Mesa in early April 1959. Scattered groups of birds occurred in Unaweep Canyon (Rogers 1964, Bailey and Niedrach 1965). Sage-grouse also occurred along the Little Dolores River into Grand County, Utah (Rogers 1964, CEB, pers. obs.). The hunting season in Mesa County was closed in 1958 (Rogers 1964), but hunting was known to occur (11 sage-grouse wings received from hunters in 1985) into the mid 1990s in Glade Park and on Pinon Mesa. Sage-grouse also occurred in the Dominguez Canyon area of the Uncompahgre Plateau as Anderson (1969) reported the population disappeared after the entire area had been sprayed with the herbicide 2, 4-D. No sage-grouse or signs of them were observed in this area during habitat surveys in 1999 (KMP, pers. obs.). Birds were present in eastern Mesa County south of the Colorado River in 1961 (Rogers 1964). Evidence (fresh droppings) of sage-grouse were reported (J. P. Beason, Rocky Mountain Bird Observatory, pers. comm.) near the community of Mesa during systematic surveys in suitable habitat during February, March, and April 2009 suggesting winter use of this area. Gunnison Sage-Grouse were radiomarked and studied in the Glade Park-Pinon Mesa area in 1995–1997 (Commons 1997).

Mineral County.—The only report of any sage-grouse in this county is that of J. D. Hart dated 1 July 1937 (in Rogers 1964:20). There is an area southeast of Creede towards South Fork that is dominated by sagebrush, which may be where sage-grouse were present in this county. It is peripherally linked to sagebrush habitats near Del Norte in Rio Grande County.

Montezuma County.—Sage-grouse were reported to be common in Montezuma County (Morrison 1888) and Sclater (1912) reported the presence of sage-grouse north and south of Cortez. Considerable numbers of birds occurred north of Narraquinep Reservoir, with a few southwest of Dolores near Ruins Canyon and the Utah line (Rogers 1964, Bailey and Niedrach 1965). Rogers (1964) reported that hunting of sage-grouse was closed in Montezuma County in 1960. A few birds were observed in 1961 east of Pleasant View, west of the Dolores River around Ruins Canyon, south of Cortez and west of U.S. Rte. 666 (present-day U.S. Rte. 491), and in the Sandstone, Hovenweep, Wood, and Yellowjacket Canyon areas (Rogers 1964). Sage-grouse persisted in this area into the mid 1990s and a hen was observed northwest of Cortez towards Hovenweep Canyon by Robin Olterman (Colorado Division of Wildlife, pers. comm.) in about 1996. This population was likely extirpated in the late 1990s.

Montrose County.—Sage-grouse were 'very common' winter residents of southwestern Montrose County (Warren 1909). Rogers (1964) reported sage-grouse occurred northwest of Norwood to near Nucla (airport). There were five

small leks with a few birds in the Cimarron drainage in the eastern part of the county (Rogers 1964, Bailey and Niedrach 1965). Sage-grouse also occurred in Bostwick Park (5 males counted on a lek in 1959), the area around Gould's Reservoir, and near the town of Maher (Rogers 1964). A few remained on Sims Mesa in April 1995 (CEB, pers. obs.) and near Colona into the mid to late 1990s. Dale Coven of the Colorado Division of Wildlife observed one male on Sims Mesa in spring 2000. This observation was followed by release of six birds at Sims Mesa in April 2000 that were captured in the Gunnison Basin. A few birds persisted on Cerro Summit with little change in numbers counted (2–5 males each year with counts) between 1959–1999.

Ouray County.—Sage-grouse were present in this county in 1961 (Rogers 1964). Sage-grouse were reported to be present in December 1989 (Ken Miller, Colorado Division of Wildlife, pers. comm.) 3 km north of Ridgway and towards Duckett Draw to Sims Mesa in Montrose County (1995–1997) into the mid to late 1990s. This population was extirpated in the late 1990s.

Pitkin County.—Rogers (1964) reported there were only 4 km^2 of sagebrush habitat in Pitkin County. Sage-grouse were counted on leks at Capitol Creek in 1960–1961 near Snowmass and were also known to occur west of the town of Carbondale in the Thompson Creek Drainage near the Garfield County line (Rogers 1964). This population was extirpated by the mid 1960s.

Saguache County.—Captain J. W. Gunnison reported grouse (species not identified) at two different locations during his travel in 1853 in the San Luis Valley north of Fort Massachusetts (Beckwith 1855). Sage-grouse were collected on Cochetopa Pass in 1858 by Captain Beckwith and Mr. Kreutzfeldt (Baird 1858). The 1855 Beckwith report describing Gunnison's travels commonly mentioned the presence of sagebrush throughout the area. This county has the second largest amount of sagebrush habitat in southwestern Colorado. Especially good habitat occurred along the Razor, Cochetopa, Gold Basin, Pole, Sugar, and Beaver Creek drainages (Rogers 1964, Bailey and Niedrach 1965).

A small population of Gunnison Sage-Grouse currently persists on the south side of Poncha Pass. Rogers (1964:116) stated the Poncha Pass area was not checked, but birds had not been reported in some time. Rogers further states the Poncha Pass area was the top choice of four possible locations in Colorado for potential transplants of sage-grouse (1964:27). These comments likely precipitated the transplant of a group of 32 birds captured on Sapinaro Mesa in the Gunnison Basin in 1971 (17) and 1972 (15), and released (by the Colorado Department of Game, Fish and Parks and the Bureau of Land Management) near Round Hill (along San Luis Creek) on the south side of Poncha Pass. At least 20 sage-grouse were harvested in this area in September 1992 when the area was accidentally opened for hunting. Gunnison Sage-Grouse were observed, radiomarked, and studied in this area during part of 1990 through 2012 (CEB, JAN, pers. obs.). Gunnison Sage-Grouse were transplanted to Poncha Pass during spring 2000 (24), spring 2001 (20), and fall 2002 (7) from the Gunnison Basin.

San Miguel County.—Bent (1932:309) reported sage-grouse from Lone Cone southeast of Norwood in San Miguel County. Rogers (1964) reported that a few occurred in the southwestern corner of the county north of Dove Creek and west of Egnar. They also occurred south of Norwood near Basin Creek, Beaver Mesa, and south of Gurley Reservoir (Rogers 1964, Bailey and Niedrach 1965). Rogers (1964:24) noted that sage-grouse in the Gregor Flats area only had between 13–26 km^2 of habitat. Gunnison Sage-Grouse were studied in this area, as well as on Hamilton Mesa, and in Dry Creek Basin in the mid to late 1990s (Commons 1997).

DISCUSSION

Gunnison Sage-Grouse were patchily distributed, frequently in linear strips along riparian areas as well as in intermountain basins in Colorado in the early 1900s. These areas, based on observations by CEB in the post 1969 period, were dominated by species of *Artemisia* (*cana, nova, tridentata tridentata, t. vaseyana*), Gambel's oak (*Quercus gambelii*), serviceberry (*Amelanchier* spp.), and snowberry (*Symphoricarpos* spp.), as well as a large variety of native forbs and taller grasses. Gunnison Sage-Grouse used smaller (<4 km^2) sagebrush-dominated openings in southwest Colorado that contained sagebrush as well as deciduous shrubs. Use of <5–6 km^2 patches of suitable habitat by radio-marked birds (Commons 1997) suggests more adaptability to heterogeneous sagebrush habitats than Greater Sage-Grouse (Connelly et al. 2011).

We view the former distribution of Gunnison Sage-Grouse in Colorado as a series of five metapopulations (a set of local populations that interact through individual movements among populations [Hanski and Gilpin 1991]) based on likely linkages among habitat patches. For example, the Colorado River metapopulation was linked to the west with the Uncompahgre Plateau metapopulation, which was linked with the Gunnison Basin metapopulation to the east and the Colorado Plateau metapopulation to the south. The San Luis Valley metapopulation was more isolated but was linked with the Gunnison Basin to the northwest (Table 2). Sagebrush-dominated corridors among these metapopulations continue to exist although they are now fragmented.

Linkages among populations of Gunnison Sage-Grouse in the mid-1990s were examined using genetic methods (Oyler-McCance et al. 2005). Of the eight subpopulations recognized by Colorado Parks and Wildlife (Oyler-McCance et al. 2005:fig. 1), seven were included in the genetic analysis. The Poncha Pass subpopulation was not included because at that time, it was the only subpopulation that had been augmented by translocations from other areas. Oyler-McCance et al. (2005) found a high degree of genetic structure and low amounts of gene flow across most subpopulations of Gunnison Sage-Grouse (the only exception being between the geographically adjacent Gunnison and Curecanti subpopulations in the Gunnison Basin). The Dove Creek/Monticello (San Juan County, Utah) and Pinon Mesa subpopulations were the most different and had the lowest levels of genetic diversity. Oyler-McCance et al. (2005) also found that the San Miguel subpopulation may act as a conduit of gene flow surrounding the larger subpopulation in the Gunnison Basin. Gunnison Sage-Grouse from Cerro/Cimarron/Sims were more closely aligned with the San Miguel subpopulation than the Gunnison or Curecanti subpopulations. The Crawford (Fruitland Mesa) subpopulation was also significantly different from surrounding populations suggesting low levels of gene flow (Oyler-McCance et al. 2005). Such patterns of genetic structure within Gunnison Sage-Grouse will change as augmentation efforts now involve moving birds from the Gunnison Basin subpopulation to maintain the other subpopulations.

The Colorado River and its tributary, the Eagle River appear to be the northern boundary of the Gunnison sage-grouse historical distribution in Colorado. Greater Sage-Grouse are known to occur immediately north of the Colorado-Eagle River system in Mesa, Garfield, and Eagle counties. Sage-grouse in these counties, as with all counties in northwestern and northcentral Colorado, were studied during the 1973–1999 interval. All were Greater Sage-Grouse (CEB, pers. obs., Hupp and Braun 1991, Oyler-McCance et al. 1999). We found no museum specimens of Greater Sage-Grouse from the area south of the Colorado-Eagle River boundary and no specimens of Gunnison Sage-Grouse from north of this boundary.

TABLE 2. Possible metapopulations of Gunnison Sage-Grouse in Colorado.

Metapopulation	Counties
Colorado River	S Eagle, Pitkin, S Garfield, E Mesa
Gunnison Basin	Gunnison, NW Saguache, Hinsdale, Delta, Montrose
Uncompahgre Plateau	Ouray, Montrose, SW Mesa, San Miguel
Colorado Plateau	Dolores, Montezuma, LaPlata, Archuleta
San Luis Valley	NE Saguache, Alamosa, Conejos, Costilla, Rio Grande

Armstrong (1972) studied ecogeographic distributions of fauna in Colorado and (page 337) reported the Colorado River and its canyons form important physical barriers and that the Grand River Valley was an important barrier. He concluded it was not only the presence of a large river system but also the diversity of the vegetation on the floor and sides of the valley that affected faunal populations north and south of the river system. It is difficult to perceive the present upper Grand Valley along the Colorado River drainage in Mesa, Garfield, and Eagle counties as a barrier to north-south movement by sage-grouse. However, we have limited knowledge of historic habitat conditions when and where the two sage-grouse species evolved.

Specimen records were found from Dolores, Gunnison, Mesa, Saguache, and San Miguel counties in Colorado. Only one of multiple sage-grouse specimens collected in the 1870s in Lake County near Twin Lakes (Henshaw 1875) was located (U.S. National Museum). A piece of toe-pad was obtained from this specimen and tested for species identification (by SJO-M) by comparing its mitochondrial haplotypes with those

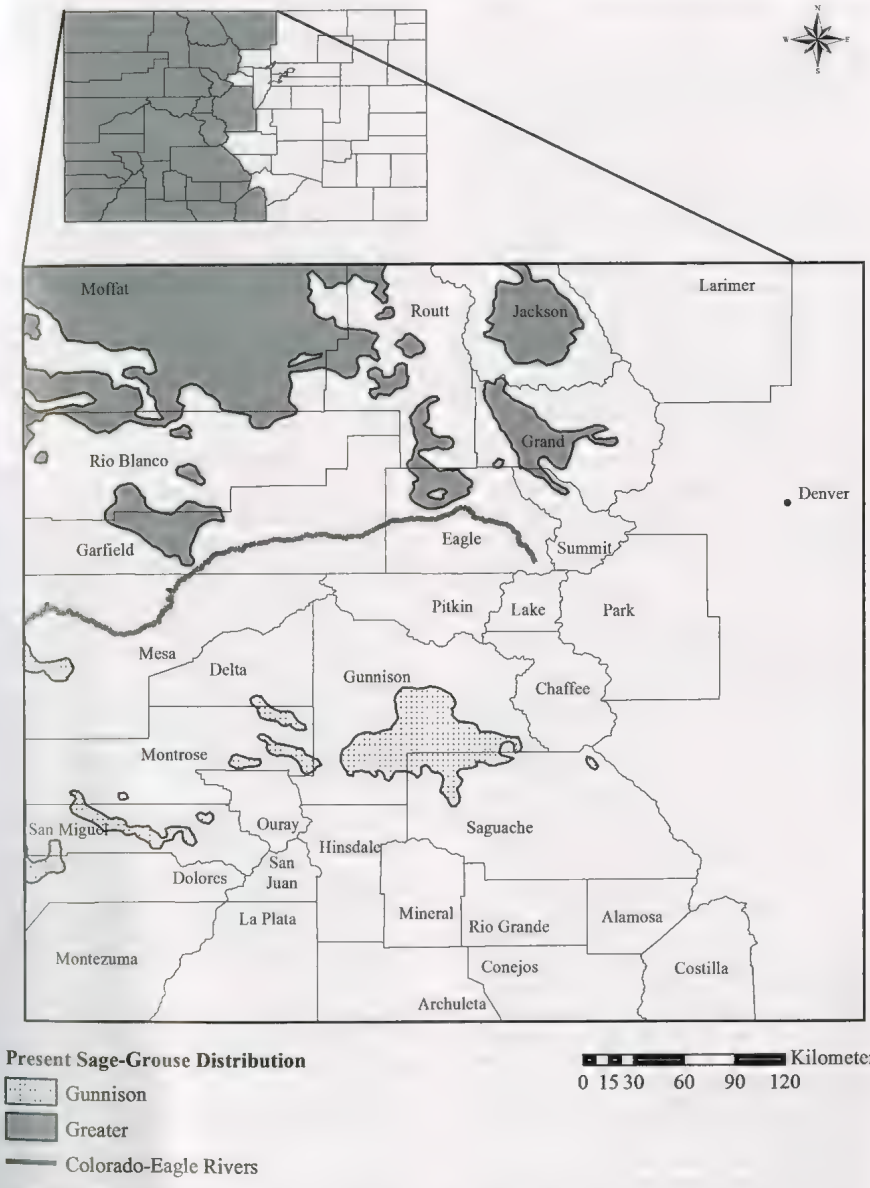


FIG. 2. Present distribution of Gunnison Sage-Grouse and Greater Sage-Grouse in Colorado (modified from Braun 1995).

published previously for both species (Oyler-McCance et al. 1999). The mitochondrial DNA haplotype from this specimen was consistent with Greater Sage-Grouse rather than Gunnison Sage-Grouse. Lake County is adjacent (north) of Chaffee County and immediately south of Summit County where Greater Sage-Grouse are known to exist. Field surveys in Park County, immediately east of Lake and Chaffee counties, where the earliest fossil sage-grouse was reported (Emslie 2004), failed to locate contemporary sagebrush communities capable of supporting sage-grouse.

The historical distribution of Gunnison Sage-Grouse included at least 20 counties (based on Braun 1995). At present, this species persists in only eight counties (Table 1, Fig. 2) in Colorado, five of which, Montrose (Cimarron), Dolores (Dove Creek), Mesa (Pinon Mesa/Glade Park), Saguache (Poncha Pass), and San Miguel (Miramonte/Dry Creek Basin) are being sustained by augmentations from the subpopulation in the Gunnison Basin. Half of the county extirpations occurred prior to or around 1945 (Alamosa, Chaffee, Conejos, Costilla, Mineral, and Rio Grande). Others occurred in the 1960s (Archuleta, Pitkin) and 1996–1998 (Eagle, Garfield, Montezuma, and Ouray) (Table 1).

The possibilities for restoration of extirpated populations or the augmentation of those presently with small populations are problematic as most historically occupied areas are no longer suitable because of habitat degradation, fragmentation, and permanent loss from agricultural activities, gas and oil development, and expansion of homes and ranchettes. The Gunnison Basin could have the greatest restoration potential given the large amount of habitat still available. The Cimarron area also has potential for increasing population size through habitat management. Areas outside of the Gunnison Basin that may be options for restoration of Gunnison Sage-Grouse, based on public land ownership and current areas with larger patches of sagebrush, are those in Dolores, Montezuma, San Miguel, Montrose, and Delta counties. Other suitable reintroduction sites might include the area east and south of Fort Garland as sagebrush habitats extend into New Mexico. CEB reviewed adjacent sagebrush-dominated areas in New Mexico in the 1970s and again in the mid 2000s and noted the lack of suitable brood habitat as well as degraded nesting habitats. Similar conditions occur in Costilla County, Colorado and any restoration attempts would need to focus on improving native understory species in nesting areas with live sagebrush, brood habitat, as well as potential winter-use areas (Connelly et al. 2011).

ACKNOWLEDGMENTS

Field work during 1977–1999 was supported by the Colorado Division of Wildlife. We thank all field personnel who helped with studies in Delta, Dolores, Gunnison, Mesa, Montrose, Saguache, and San Miguel counties, especially Area Wildlife Manager Jim Houston, Wildlife Managers Cliff Coghill, Dale Coven, Dave Harper, Doug Homan, Bill Heicher, Dave Kenvin, and Maurice Potter, and Wildlife Biologist Jim Olterman. We thank Joanne Saher for her insightful comments on the manuscript and for help with figures. We also thank two anonymous referees for helpful reviews of the manuscript. This is a contribution from Federal Aid to Wildlife Restoration projects W-152-R and W-167-R.

LITERATURE CITED

ANDERSON, A. E. 1969. 2, 4-D, sagebrush, and mule deer-cattle use of upper winter range. Colorado Division of Game, Fish and Parks Special Report. Number 21.

ARMSTRONG, D. M. 1972. Distribution of mammals in Colorado. Museum of Natural History Monograph. Number 3. University of Kansas, Lawrence, USA.

BAILEY, A. M. AND R. J. NIEDRACH. 1965. Birds of Colorado. Volume 1. Denver Museum of Natural History, Denver, Colorado, USA.

BAIRD, S. F. 1858. Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. Volume IX, Beverly Tucker, Printer. Washington, D.C., USA.

BECKWITH, E. G. 1855. Report upon the route near the Thirty-Eight and Thirty-Ninth Parallels explored by Captain J. W. Gunnison. Chapters III and IV. Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean, made under the direction of the Secretary of War, in 1853–1854. Volume II. U.S. Government Printing Office, Washington, D.C., USA.

BENT, A. C. 1932. Life histories of North American gallinaceous birds. Orders Galliformes and Columbiformes. U.S. National Museum Bulletin 162.

BERGTOLD, W. H. 1928. A guide to Colorado birds. Smith-Brooks Printing Co., Denver, Colorado, USA.

BRAUN, C. E. 1995. Distribution and status of sage grouse in Colorado. Prairie Naturalist 27:1–9.

COMMONS, M. L. 1997. Movement and habitat use by Gunnison Sage Grouse in southwestern Colorado. Thesis. University of Manitoba, Winnipeg, Canada.

COMMONS, M. L., R. K. BAYDACK, AND C. E. BRAUN. 1999. Sage grouse response to pinyon-juniper management. Pages 238–239 *in* Proceedings: ecology and management of pinyon-juniper communities within the Interior West (S. B. Monsen and R. Stevens,

Compilers). USDA, Forest Service, RMRS-P-9. Rocky Mountain Research Station, Ogden, Utah, USA.

CONNELLY, J. W., E. T. RINKES, AND C. E. BRAUN. 2011. Characteristics of Greater Sage-Grouse habitats: a landscape species at micro- and macroscales. Pages 69–83 *in* Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats (S. T. Knick and J. W. Connelly, Editors). Studies in Avian Biology. Volume 38.

COOKE, W. W. 1897. The birds of Colorado. State Agricultural College, Agricultural Experiment Station Bulletin 37, Technical Series 2. Smith-Brooks Printing Co., Denver, Colorado, USA.

COUES, E. 1898. The journal of Jacob Fowler. Francis P. Harper, New York, USA.

EMSLIE, S. D. 2004. The early and middle Pleistocene avifauna from Porcupine Cave, Colorado. Early and middle Pleistocene biodiversity and environmental change: the Porcupine Cave fauna from Colorado (A. D. Barnowsky, Editor). University of California Press, Berkeley, USA.

GUNNISON SAGE-GROUSE RANGEWIDE STEERING COMMITTEE. 2005. Gunnison Sage-Grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, USA.

HANSKI, I. AND M. GILPIN. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

HENSHAW, H. W. 1875. Report on ornithological collections made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 1871, 1872, 1873, and 1874. *In* Report upon geographical and geological explorations and surveys west of the one hundredth meridian (First Lieut. George M. Wheeler, Corps of Engineers, in charge). 6 Volumes. Government Printing Office, Washington, D.C., USA.

HUPP, J. W. 1987. Sage grouse resource exploitation and endogenous reserves in Colorado. Dissertation. Colorado State University, Fort Collins, USA.

HUPP, J. W. AND C. E. BRAUN. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53:823–829.

HUPP, J. W. AND C. E. BRAUN. 1991. Geographic variation among sage grouse in Colorado. Wilson Bulletin 103:255–261.

MORRISON, C. F. 1888. A list of the birds of La Plata County, Colorado. Ornithologist and Oologist 13:70–75,107–108, 115–116, 139–140, 145–148, 165–168, 181–183.

OYLER-MCCANCE, S. J. 1999. Genetic and habitat factors underlying conservation strategies for Gunnison Sage Grouse. Dissertation. Colorado State University, Fort Collins, USA.

OYLER-MCCANCE, S. J., N. W. KAHN, K. P. BURNHAM, C. E. BRAUN, AND T. W. QUINN. 1999. A population genetic comparison of large- and small-bodied Sage Grouse in Colorado using microsatellite and mitochondrial DNA markers. Molecular Ecology 8:1457–1465.

OYLER-MCCANCE, S. J., K. P. BURNHAM, AND C. E. BRAUN. 2001. Influence of changes in sagebrush on Gunnison Sage Grouse in southwestern Colorado. Southwestern Naturalist 46:323–331.

OYLER-MCCANCE, S. J., J. St. JOHN, S. E. TAYLOR, A. D. APA, AND T. W. QUINN. 2005. Population genetics of Gunnison Sage-Grouse: implications for management. Journal of Wildlife Management 69:630–637.

ROCKWELL, R. R. 1908. An annotated list of the birds of Mesa County, Colorado. Condor 10:152–180.

ROGERS, G. E. 1964. Sage Grouse investigations in Colorado. Colorado Game, Fish and Parks Department Technical Publication. Number 16.

SCHROEDER, M. A., C. L. ALDRIDGE, A. D. APA, J. R. BOHNE, C. E. BRAUN, S. D. BUNNELL, J. W. CONNELLY, P. A. DEIBERT, S. C. GARDNER, M. A. HILLIARD, G. D. KOBRIGER, S. M. MCADAM, C. W. MCCARTHY, J. J. MCCARTHY, D. L. MITCHELL, E. V. RICKERSON, AND S. J. STIVER. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

SCLATER, W. L. 1912. A history of the birds of Colorado. Witherby and Co., London, UK.

U.S. DEPARTMENT OF INTERIOR (USDI). 2013. Endangered and threatened wildlife and plants; endangered status for Gunnison Sage-Grouse. U.S. Department of the Interior, Fish and Wildlife Service. Federal Register 78:2485–2538.

WARREN, E. R. 1909. Notes on the birds of southwestern Montrose County, Colorado. Condor 11:11–17.

WARREN, E. R. 1916. Notes on the birds of the Elk Mountain region, Gunnison County, Colorado. Auk 33:292–317.

YOUNG, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence of Sage Grouse. Dissertation. Purdue University, West Lafayette, Indiana, USA.

YOUNG, J. R., J. W. HUPP, J. W. BRADBURY, AND C. E. BRAUN. 1994. Phenotypic divergence of secondary sexual traits among Sage Grouse, *Centrocercus urophasianus*, populations. Animal Behavior 47: 1353–1362.

YOUNG, J. R., C. E. BRAUN, S. J. OYLER-MCCANCE, J. W. HUPP, AND T. W. QUINN. 2000. A new species of Sage Grouse (Phasianidae: *Centrocercus*) from southwestern Colorado. Wilson Bulletin 112:445–453.

The Wilson Journal of Ornithology 126(2):218–235, 2014

PHYLOGEOGRAPHY OF THE GAMBEL'S QUAIL (*CALLIPEPLA GAMBELII*) OF WESTERN NORTH AMERICA

DAMON WILLIFORD,[1,5] RANDY W. DEYOUNG,[1] RODNEY L. HONEYCUTT,[2] LEONARD A. BRENNAN,[1] FIDEL HERNÁNDEZ,[1] JAMES R. HEFFELFINGER,[3] AND LOUIS A. HARVESON[4]

ABSTRACT.—We conducted a phylogeographic study of the Gambel's Quail (*Callipepla gambelii*) using sequences of the mitochondrial control region and NADH dehydrogenase subunit 2 (ND2) obtained from 167 specimens including hunter–harvested wings and museum study skins. The Gambel's Quail exhibited strong phylogeographic structure, large genetic gaps, and relatively high levels of haplotype ($Hd = 0.79$) and nucleotide diversity ($\pi = 0.01$). Thirty-four Gambel's Quail haplotypes clustered into two distinct haplogroups, with two additional highly divergent haplotypes. Distribution of the haplogroups was not concordant with sampled subspecies or ecogeographic regions; however, the overall distribution of the two haplogroups suggests that the Gambel's Quail may have been isolated in separate refugia of the Chihuahuan and Sonoran deserts during the Pleistocene. Both haplogroups appear to have undergone recent demographic expansion, possibly related to climatic changes associated with the onset of drier conditions in southwestern North America following the end of the Last Glacial Maximum. *Received 17 July 2013. Accepted 7 December 2013.*

Key words: *Callipepla gambelii*, Gambel's Quail, mitochondrial DNA, phylogeography, population structure.

Gambel's Quail (*Callipepla gambelii*) is a common resident of brushland and thorn-scrub habitats of southwestern North America. The geographic range of Gambel's Quail is centered in the Sonoran Desert and extends to adjacent parts of the Mojave and Chihuahuan deserts and southwestern California and Baja California (Brown et al. 1998, Fig. 1). The California Quail (*C. californica*) is regarded as a sister species of the Gambel's Quail, and both species have highly similar plumages. Gambel's and California quails are part of the crested quail complex that also includes the Elegant Quail (*C. douglasii*) and Scaled Quail (*C. squamata*).

The seven subspecies of Gambel's Quail were described based on slight variations of male plumage coloration, differences in body size, and geography. However, the taxonomic validity of some subspecies has been questioned (Hellmayr and Conover 1942, Ridgway and Friedmann 1946, Pitelka 1948, Madge and McGowan 2002). *Callipepla g. gambelii* has the widest range, occurring throughout the Sonoran Desert and adjacent areas, whereas the other subspecies have more limited ranges. *C. g. ignoscens* occurs in southeastern New Mexico and western Texas (Chihuahuan Desert), while the ranges of three other subspecies (*fulvipectus*, *friedmanni*, and *stephensi*) are restricted to parts of Sonora. *C. g. pembertoni* is found only on Tiburón Island in the Gulf of California off the coast of Sonora. The allopatric *C. g. sana* is endemic to southwestern Colorado.

The taxonomy and biogeography of the Gambel's Quail has received little recent attention, and genetic studies of this species are limited. Gambel's, California, and Elegant quails were formerly placed in the genus *Lophortyx*, but were considered to be the closest living relatives of the Scaled Quail (Holman 1961). Electrophoretic data (Gutíerrez et al. 1983) and mitochondrial DNA (mtDNA) sequences (Zink and Blackwell 1998) confirmed that the Gambel's, California, Elegant, and Scaled quails were more closely related to one another than to other New World quails. All four *Callipepla* species are thought to have diverged during the late Cenozoic (Hubbard 1973, Gutíerrez et al. 1983, Zink et al. 1987, Zink and Blackwell 1998).

A species that is characterized by low dispersal (<2 km), short–life span, and high population turnover such as the Gambel's Quail (Brown et al. 1998) should display high degree of phylogenetic structure throughout its range (Harrison and Hastings 1996, Avise 2000). Therefore, one major prediction would be that patterns of mtDNA variation in Gambel's Quail should show consid-

[1] Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, TX 78363, USA.
[2] Natural Science Division, Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263, USA.
[3] Arizona Game and Fish Department, 555 N. Greasewood Road, Tucson, AZ 85745, USA.
[4] Borderlands Research Institute, Sul Ross University, P. O. Box C–16, TX 79832, USA.
[5] Corresponding author; e-mail: rook137@gmail.com

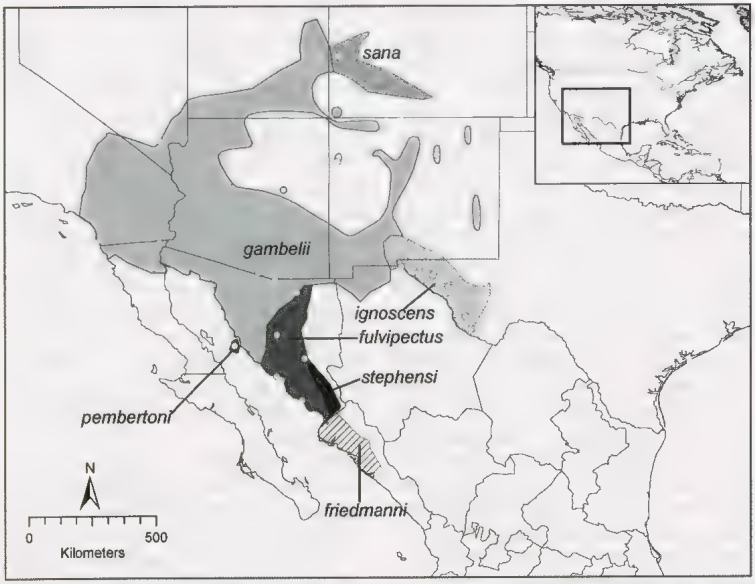


FIG. 1. Geographic distribution of the Gambel's Quail and its subspecies. Geographic distributions of each subspecies were based on modified ARCMAP shapefile of the range of the Gambel's Quail provided by Ridgely (2007). Subspecies boundaries were determined by data from Texas Game, Fish and Oyster Commission (1945), Ridgway and Friedmann (1946), Johnsgard (1988), and Madge and McGowan (2002).

erable phylogeographic structure. Our specific objectives were to: 1) test for patterns of phylogeographic structure throughout the range of the Gambel's Quail, 2) explore its demographic history, and 3) assess the genetic distinctiveness of the various subspecies of the Gambel's Quail.

METHODS

Sample Collection.—Between 2008–2010, we obtained contemporary samples (wings or feathers) of hunter–harvested Gambel's Quail from Arizona (Gila County, $n = 11$; Pinal County, $n = 39$), Utah (Washington County, $n = 17$), and New Mexico (Luna County, $n = 7$; Sierra County, $n = 2$). We also included contemporary samples of Gambel's Quail from Texas (Hudspeth County, $n = 19$; Presidio County, $n = 18$; Culberson County, $n = 9$) that had been collected 2002–2004 by Sullins (2006), and DNA extracted from blood from Gambel's Quail trapped at the Buenos Aires National Wildlife Refuge, Arizona ($n = 7$) in 2004. We supplemented the contemporary samples with tissues (toepad skin or feathers) obtained from museum specimens (online Supplemental Materials). Toepad samples consisted of small ($3 \times 1 \times 1$ mm) pieces of skin excised from the ventral side of the foot using a sterile razor or scalpel blade (changed for each specimen) (Mundy et al. 1997). Each sample was placed in either a sterile, 2.0–mL tube with a screw cap or a small Ziploc bag and stored at room temperature. We obtained tissue samples of California Quail, including hunter–harvested birds from Lake County, Oregon ($n = 6$) and Franklin ($n = 8$), Okanagan ($n = 8$), Walla Walla ($n = 5$), Yakima ($n = 8$) counties, and museum specimens (online Supplemental Materials), for use as outgroups and to detect hybridization where the ranges of California and Gambel's quails overlap. We also acquired tissue samples of three additional species of New World quails for use as outgroups in phylogenetic analysis, including a museum specimen of Elegant Quail (online Supplemental Materials) and hunter–harvested specimens of a Scaled Quail from Culberson County, Texas and a Northern Bobwhite (*Colinus virginianus*) from Goliad County, Texas.

Extraction.—Contamination represents a serious problem when working with DNA extracted

from museum specimens (Mulligan 2005). We developed an anti–contamination protocol based on guidelines from Hummel (2003), Pääbo et al. (2004), and Mulligan (2005). All DNA extractions from museum specimens and pre–amplification set–up procedures for those samples were carried out in a separate laboratory where no previous work on contemporary galliforms had been conducted. Separate equipment and supplies were used for museum and contemporary samples. Equipment and benchtops were sterilized with 20% bleach solution or DNA Away (Molecular BioProducts, San Diego, California) prior to use. Small equipment and supplies were sterilized with ultraviolet light for 1 hr. We adopted a "one-way traffic" protocol that prevented entry into the museum–specimen laboratory on the same day after conducting work in the "contemporary" DNA lab. We extracted DNA from ≤10 museum specimen samples at a time to minimize the risk of mistakes. We used 1–2 negative extraction controls for each round of extraction, and 1–3 negative controls each round of amplification, with polymerase chain reaction (PCR).

We extracted genomic DNA using the DNeasy® Blood & Tissue Kit and tissue protocol (Qiagen, Valencia, California). We altered the Tissue Protocol to maximize the amount of DNA obtained from historical samples. We increased the amount of proteinase K added to each sample from 20 µL to 30 µL. To increase the yield of DNA, we conducted the final elution step using a solution of diluted elution buffer (1 part buffer, 2 parts double–deionized water) to obtain a volume of 150 µL. Final elutions were then vacuum–centrifuged at 30 °C to a final volume of 50 µL to increase DNA concentration.

Amplification and Sequencing.—Because of its small effective population size and fast coalescence time, mtDNA is the leading indicator of intraspecific lineage divergence (Avise 2000, Zink and Barrowclough 2008, Barrowclough and Zink 2009). The mitochondrial control region (Vigilant et al. 1991, Wenink et al. 1994) and NADH dehydrogenase subunit 2 (ND2; Hackett 1996, Omland et al. 1999) display high levels of variability, making both useful as genetic markers for studies of recently diverged populations. Primers L16755 (5′ TAC GGC TTG AAA AGC CAT TG 3′; Nedbal et al. 1997) and OSU7713 (5′ CCT GAC CGA GGA ACC AGA GGC GC 3′; Van Den Bussche et al. 2003) were used to amplify 500 bp of the highly variable 5′ region I of the control region. However, these primers performed poorly on tissue samples from museum study skins. Therefore, we designed a pair of internal primers, NBW222F (5′ CTA AGC CCA TTG TAT GTA CAC GGA 3′) and NBW222R (5′ GGG TAC GAC CAA TAA ATC CAT CTG 3′). These primers were originally designed for museum specimens of bobwhites (*Colinus* spp.), but performed equally well on Gambel's, California, and Elegant quails. We used these internal primers to amplify a ~224-bp fragment of the most highly variable portion of the segment amplified by L16755 and OSU7713. Primers H5578 (5′ CCT TGA AGC ACT TCT GGG AAT CAG A 3′) and L5215 (5′ TAT CGG GCC CAT ACC CCG AAA AT 3′; Hackett 1996) were used to amplify 360 bp of the ND2 gene of all specimens.

Polymerase chain reactions were conducted in 25–µL reaction volumes containing 1.5–3.0 µL of total genomic DNA, 12.5 µL of AmpliTaq® Gold PCR Master Mix (Applied Biosystems, Forest City, California), 10.0 pmol of each primer, 1.0 µL of bovine serum albumin (2 mg/mL), and sufficient double–deionized water to reach the final volume. Amplification was performed using an ABI 2720 thermal cycler (Applied Biosystems) with the following protocol: initial denaturation at 94.0 °C for 10.0 min, 35 cycles of denaturation at 94.0 °C for 50.0 sec, annealing at 61 °C for 1.0 min, extension at 72.0 °C for 2.0 min, and a final extension at 72.0 °C for 30.0 min.

All PCR products were electrophoresed on a 1% agarose gel containing ethidium bromide and viewed under UV light to verify successful amplification. Amplification products were purified by an enzymatic method (ExoSAP–IT™, USB Corporation, and Wilmington, Maryland) and sequenced using the ABI BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems). Dye terminators were removed with the DyeEx 2.0 Spin Kit and protocol (Qiagen). Sequence reaction products were loaded on an ABI Prism 3130 Genetic Analyzer (Applied Biosystems) for separation and detection. Mitochondrial DNA sequences were edited in SEQUENCHER Version 4.6 (GeneCodes, Ann Arbor, Michigan), and aligned using CLUSTAL X Version 2.1 (Larkin et al. 2007). We trimmed control region sequences from contemporary specimens to the same length as those from museum specimens. Control region and ND2 sequences were concatenated using the program SEQUENCEMATRIX 1.7.8 (Vaidya

et al. 2011). Mitochondrial DNA sequences of Gambel's and California quail and outgroup taxa were deposited in GenBank as accession numbers KC556212–KC556268, KC556326–KC556486, KC556166, KC556168, KC556741 (control region); and KC556269–KC556325, KC556576–KC556736, KC556191, KC556204, and KC556747 (ND2).

Data Analysis.—We grouped samples from Gambel's Quail by county (United States) or municipality (Mexico). Samples were then subdivided into subspecies based on geographic data and the range of each subspecies (Ridgway and Friedmann 1946, Brown et al. 1998, Madge and McGowan 2002). We computed haplotype diversity (*Hd*) and nucleotide diversity (π, Nei 1987) for each subspecies and states from which specimens were collected with the computer program DNASP Version 5.10.01 (Librado and Rozas 2009). We also computed haplotype and nucleotide diversity for museum and contemporary samples and for any distinct groups of haplotypes observed. We examined relationships among the haplotypes by constructing a minimum spanning tree (Kruskal 1956, Prim 1957) in ARLEQUIN Version 3.5 (Excoffier and Lischer 2010). ARLEQUIN computes the minimum spanning tree from a matrix of the absolute number of differences (i.e., substitutions; Excoffier and Smouse 1994), calculated among all pairs of haplotypes using a modification the algorithm described in Rohlf (1973). We used the program HAPSTAR Version 0.6 (Teacher and Griffiths 2011) to draw the minimum spanning tree. The minimum spanning tree was edited in the program INKSCAPE Version 0.48 (www.inkscape.org). We also analyzed the relationships among haplotypes by constructing a phylogenetic tree using maximum likelihood in the computer program MEGA5 (Tamura et al. 2011). The phylogenetic analysis was based on the HKY (Hasegawa et al. 1985) model with a gamma distribution and invariant sites, which was selected as the best model of nucleotide substitution based on the Akaike's (1974) information criterion (AIC) and phyML (Guindon and Gascuel 2003) maximum likelihood calculations implemented in the computer program jMODELTEST Version 2.0 (Darriba et al. 2012). The maximum likelihood analysis was conducted using the subtree–pruning–regrafting heuristic search method as implemented in MEGA5, and the reliability of the inferred relationships was assessed using 1,000 bootstrap (Felsenstein 1985) replicates.

We tested the null hypothesis that the Gambel's Quail is a panmictic species using analysis of molecular variance (AMOVA; Excoffier et al. 1992) in the computer program ARLEQUIN. Panmixia is the lack of population structure. If the Gambel's Quail is a panmictic species, all measures of genetic differentiation among populations and groups of populations will be essentially zero. We performed two separate AMOVAs with different grouping schemes. First, we grouped populations as subspecies to determine how much genetic variation was because of subspecies taxonomy. Secondly, we grouped populations as geographic groups (Texas, Arizona, Sonora, California–Baja California, New Mexico–Colorado, and Utah–Nevada) to determine how much genetic variation was because of geography. Variance components were used to calculate phi–statistics (Φ, analogous to Wright's *F* statistics; Excoffier et al. 1992), which summarize the degree of differentiation among groups (Φ_{CT}), among populations within groups (Φ_{SC}), and within populations (Φ_{ST}). Statistical significance of the variance components were assessed using 16,000 bootstrap replicates.

Genetic structure is often a consequence of isolation by distance, in which the degree of genetic similarity declines with increasing geographic distance. We investigated the relationship between geographic and genetic distances using Mantel (1967) tests implemented in the Isolation by Distance web service (IBDWS Version 3.23, ibdws.sdsu.edu; Jensen et al. 2005, Ngan 2006). The Mantel test examines whether a matrix of pairwise genetic distances is correlated with a matrix of pairwise geographic distances. We performed separate Mantel tests using F_{ST} and Φ_{ST} as the measure of genetic distance. We excluded all populations represented by only a single individual (IBDWS allows only one population to be represented by a single individual). The shortest distances (km) between populations were calculated from decimal degrees using a modified version of the haversine formula (Sinnott 1984) implemented in the computer program GenAlex Version 6.5 (Peakall and Smouse 2012). Negative genetic distances were set to zero as were the genetic distances between populations fixed for the same haplotype. We assessed the statistical significance of the Mantel tests using 16,000 bootstrap replicates.

Historical demography of a species can be inferred by computing the distribution of observed pairwise nucleotide differences or mismatch distributions of mtDNA haplotypes (Rogers and Harpending 1992). A unimodal observed mismatch distribution is an indication of sudden demographic expansion, whereas bimodal or multimodal mismatch distributions imply demographic equilibrium or decline (Rogers and Harpending 1992). We used DNASP to compute the expected mismatch distribution under a model of constant population size (Watterson 1975, Slatkin and Hudson 1991, Rogers and Harpending 1992) and the observed mismatch distributions for major intraspecific groups of the Gambel's Quail. We evaluated the statistical support for demographic expansion or stability using the mean absolute error (MAE, Rogers et al. 1996) and the raggedness index (r, Harpending 1994). The mean absolute error is the goodness of fit between the observed and the expected mismatch distributions, where MAE approaches zero as the observed distribution approaches the expected distribution. The raggedness index quantifies the smoothness of the observed mismatch distribution, where small r values are typical of expanding populations; stationary or declining populations exhibit higher values.

We also evaluated the population history of the Gambel's Quail by computing Fu's (1997) F_S, which is the most powerful test statistic for detecting population growth in large samples and non–recombining DNA sequences (Ramos–Onsins and Rozas 2002, Ramírez–Soriano et al. 2008). This test statistic is based on the probability that of the number of haplotypes in a random sample is greater than the observed number of samples drawn from a constant–sized population. Large negative values of Fu's F_S indicate an excess of haplotypes as would be expected from demographic expansion. Positive values of Fu's F_S may be caused by demographic contractions, bottlenecks, or population subdivision (Fu 1997, Ramírez–Soriano et al. 2008).

Fu's F_S, MAE, and r statistics were performed using DNASP. We tested the null hypothesis of selective neutrality by constructing 95% confidence intervals for r and Fu's F_S. Demographic expansion was supported when selective neutrality was rejected by significant small values of r ($P < 0.05$) and significant negative values of Fu's F_S ($P < 0.02$). Fu's F_S is considered significant, only if $P < 0.02$, since the 5% significance level of F_S corresponds to the lower second percentile of the empirical distribution (Fu 1997). Confidence intervals were obtained with 1,000 coalescent simulations based on a neutral infinite–sites model, assuming large constant population size (Hudson 1990). Coalescent simulations were performed using the coalescent sampler implemented in DNASP. The coalescent sampler uses the *ran1* routine (Press et al. 1992) as a random number generator and a modified version of the *make_tree* algorithm (Hudson 1990) to generate a genealogy of haplotypes.

RESULTS

We obtained 219 bp of the control region and 345 bp of ND2 for 167 Gambel's Quail, and we successfully sequenced 40 of 48 museum specimens of Gambel's Quail. No contamination was detected in any of the negative extractions or PCR controls. The final concatenated set of control region and ND2 sequences was 564 bp.

We found 48 haplotypes, 36 of which occurred in Gambel's Quail (Fig. 2). Gambel's Quail exhibited moderately high haplotype diversity ($Hd = 0.79$) and low nucleotide diversity ($\pi = 0.01$; Table 1). Haplotype and nucleotide diversity of *C. g. gambelii* and *C. g. fulvipectus* were also relatively high ($Hd \geq 0.6$, $\pi \geq 0.01$), whereas *C. g. ignoscens* (western Texas) exhibited low levels of genetic diversity ($Hd = 0.32$, $\pi < 0.001$). California and Baja California also displayed low haplotype diversity ($Hd = 0.42$), although nucleotide diversity ($\pi = 0.01$) was higher than in Texas. The highest values of haplotype and nucleotide diversity ($Hd \geq 0.70$, $\pi = 0.01$) were found in Arizona, Utah–Nevada, and New Mexico–Colorado.

There were two distinct groups of Gambel's Quail haplotypes (Haplogroups 1 and 2) and two outlier haplotypes (AA and DD; Figs. 2, 3). Seven to eight mutational steps separated the haplogroups and outlier haplotypes from one another, and eight mutational steps separated the Gambel's Quail from the California Quail. More haplotypes occurred in Haplogroup 1 ($n = 24$) than Haplogroup 2 ($n = 12$). Haplotype and nucleotide diversity was slightly greater in Haplogroup 2 ($Hd = 0.942 \pm 0.037$ SD, $\pi = 0.005 \pm 0.0005$ SD) than in Haplogroup 1 ($Hd = 0.732 \pm 0.035$ SD, $\pi = 0.003 \pm 0.0002$ SD). Neither of these haplogroups was concordant with subspecies ranges or biogeographic barriers; however, Haplogroup 2 was concentrated in the western portion

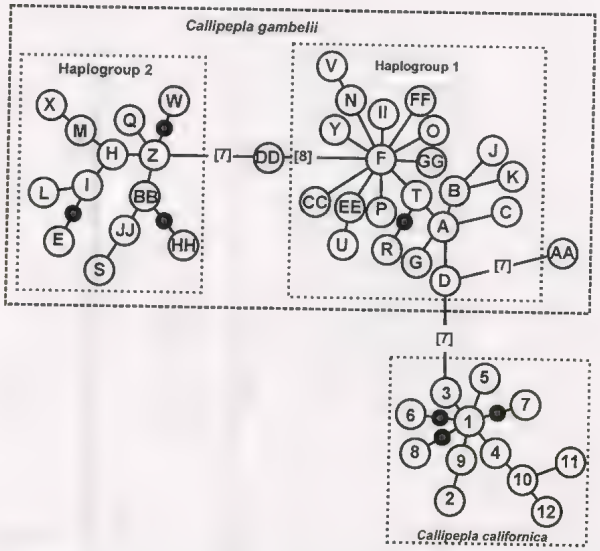


FIG. 2. Minimum spanning tree representing the phylogeographic structure of the Gambel's Quail in relation to the California Quail based on 218 concatenated sequences of the mitochondrial control region and ND2 (564 bp). Each white circle represents a unique haplotype, each line represents a single base substitution, and solid black circles are inferred missing haplotypes.

of the range, while the eastern edge of the range was dominated by Haplogroup 1 (Fig. 4). The two haplogroups of the Gambel's Quail formed star–like clusters of closely related haplotypes, with most haplotypes separated from their nearest neighbors by a single mutational step. "Private" haplotypes, those unique to specific subspecies, occurred in *C. g. gambelii* (n = 27) and *C. g. fulvipectus* (n = 5, Table 2). *Callipepla g. sana* possessed a unique haplotype. The *C. g. ignoscens* and *C. g. pembertoni* lacked unique haplotypes. Haplotype F was the most abundant and occurred in 71 individuals. Haplotype A, the second most common haplotype (n = 22), was more widespread geographically, and occurred in 14 localities (Table 3). Haplotype 4 occurred in all sampled subspecies ranges except *C. g. sana*, while haplotype F occurred in only *C. g. gambelii*

TABLE 1. Estimates of genetic diversity of the Gambel's Quail. Data are provided for sampled subspecies ranges and states including number of individual sequences (n), number of haplotypes (h), number of variable sites (S), haplotype diversity (Hd, with standard deviation), and nucleotide diversity (π with standard deviation).

	n	h	S	$Hd \pm$ SD	$\pi \pm$ SD
Callipepla gambelii	167	36	35	0.794 ± 0.029	0.009 ± 0.0011
C. g. gambelii	108	30	33	0.883 ± 0.022	0.011 ± 0.0014
C. g. fulvipectus	6	6	19	1.000 ± 0.096	0.016 ± 0.0043
C. g. ignoscens (Texas)	49	3	2	0.321 ± 0.079	0.001 ± 0.0002
C. g. pembertoni	3	2	1	0.667 ± 0.314	0.001 ± 0.0006
C. g. sana	1	1			
Arizona	65	22	28	0.792 ± 0.051	0.010 ± 0.0018
Utah-Nevada	19	6	22	0.737 ± 0.083	0.015 ± 0.0027
California-Baja California	9	3	18	0.417 ± 0.191	0.007 ± 0.0046
New Mexico-Colorado	12	7	23	0.909 ± 0.056	0.013 ± 0.0044
Sonora	13	9	21	0.872 ± 0.091	0.009 ± 0.0037

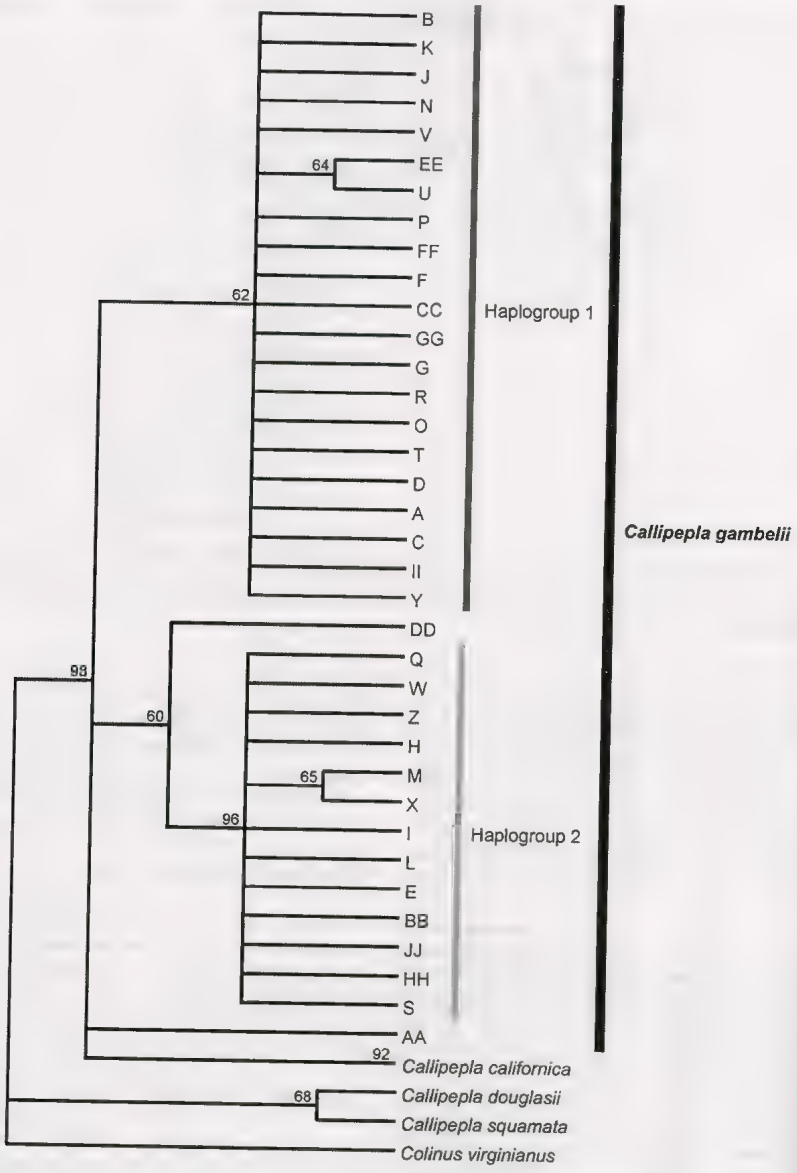


FIG. 3. Phylogenetic relationships of haplotypes of the Gambel's Quail as indicated by maximum likelihood analysis of concatenated mitochondrial control region and ND2 sequences (564 bp). Numbers represent bootstrap values (%) of adjacent nodes. Only nodes with posterior probability support ≥50% are labeled.

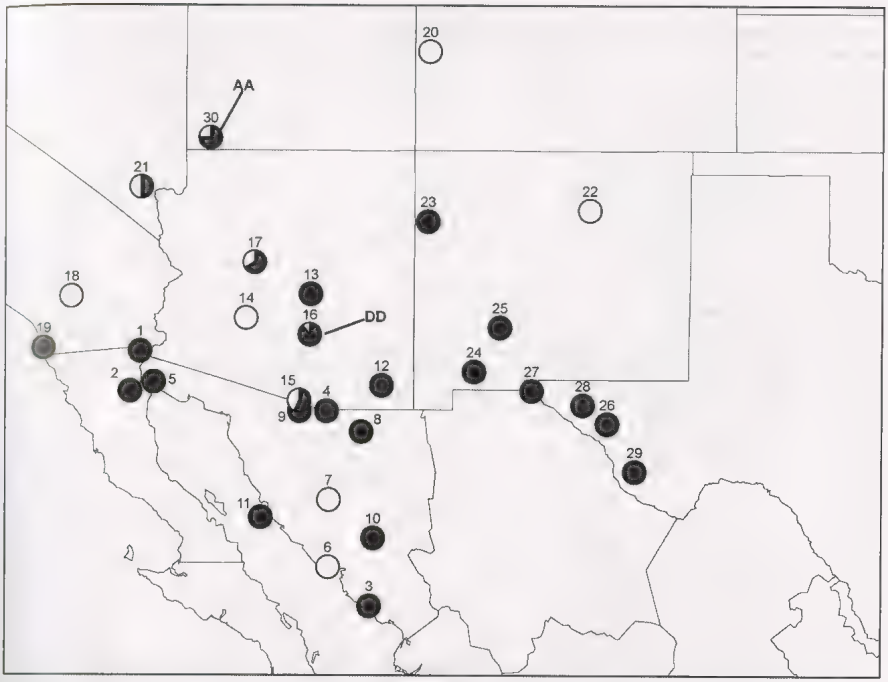


FIG. 4. Geographic distribution of Haplogroup 1 (dark gray) and Haplogroup 2 (light gray) throughout the range of Gambel's Quail. Numbers represent individual populations (Table 3), and size of pie slices indicate relative frequency of each haplogroup at each locality. Bold-faced letters represent the outlier haplotypes, AA and DD, with leader lines indicating in which locality each was found.

and *C. g. ignoscens*. The two outlier haplotypes, AA and DD, occurred only in *C. g. gambelii* and each was carried by a single individual. Haplotype AA occurred in Washington County, Utah, and haplotype DD occurred in Pinal County, Arizona.

Among the Gambel's Quail, 21 haplotypes occurred among the 127 contemporary samples collected 1999–2010 and 17 haplotypes among the 40 museum samples collected 1884–1953. Only two haplotypes (F and T) were shared among the museum and contemporary samples. Haplotypes F and T were each carried by a single museum specimen, while 70 contemporary specimens carried haplotype F and 10 contemporary specimens carried haplotype T. Haplotype and nucleotide diversity were similar among the

TABLE 2. Distribution of haplotypes among Gambel's Quail subspecies including the number of shared haplotypes (haplotypes found in >1 subspecies) and private haplotypes (haplotypes found in only 1 subspecies) for each subspecies.

Subspecies	Shared haplotypes (*n*)	Private haplotypes (*n*)
fulvipectus	A (1)	C (1), D (1), J (1), M (1), X (1)
gambelii	A (16), F (31), G (1), T (5)	B (2), E (1), H (1), I (1), K (1), L (1), N (5), O (6), P (1), Q (2), R (2), S (3), U (4), V (1), W (1), Y (9), Z (4), AA (1), BB (1), CC (2), DD (1), EE (1), FF (1), GG (1), H (1), II (1)
ignoscens	A (3), F (40), T (6)	
pembertoni	A (2), G (1)	
sana		JJ (1)

TABLE 3. Geographic distribution of Gambel's Quail haplotypes. Numbers in parentheses represent the number of individuals in each population that carried each haplotype.

Pop. no.	Locality	Haplogroup 1	Haplogroup 2	Outliers
1	Mexico: Baja California (Gardner's Lagoon and Seven Wells)	A (2), K (1)		
2	Mexico: Baja California (Mexicali)	A (4)		
3	Mexico: Sonora (Bahia Tobari)	A (1)		
4	Mexico: Sonora (Cabrero)	C (1), D (1)		
5	Mexico: Sonora (El Doctor)	T (1)		
6	Mexico: Sonora (Guaymas)		M (1)	
7	Mexico: Sonora (Pesqueira)		X (1)	
8	Mexico: Sonora (Santa Bárbara)	J (1)		
9	Mexico: Sonora (Sasabe)	A (1), B (1)		
10	Mexico: Sonora (Tecoripa)	A (1)		
11	Mexico: Sonora (Tiburon Island)	A (2), G (1)		
12	USA: Arizona (Cochise County)	A (2), B (1), F (1)		
13	USA: Arizona (Gila County)	F (8), O (1), T (1), V (1)		
14	USA: Arizona (Maricopa County)	E (1)		
15	USA: Arizona (Pima County)	F (1), G (1), R (2), S (3)		
16	USA: Arizona (Pinal County)	F (19), N (5), O (2), P (1), T (1), CC (2), EE (1), FF (1), GG (1), II (1)	Q (2), BB (1), II (2)	DD (1)
17	USA: Arizona (Yavapai County)	A (2)	I (2)	
18	USA: California (Riverside County)		H (1)	
19	USA: California (San Diego County)	A (1)		
20	USA: Colorado (Mesa County)		JJ (1)	
21	USA: Nevada (Clark County)	A (1)	W (1)	
22	USA: New Mexico (Catron County)		L (1)	
23	USA: New Mexico (Grant County)	A (2)		
24	USA: New Mexico (Luna County)	F (1), T (1), U (4)		
25	USA: New Mexico (Sierra County)	F (1), T (1)		
26	USA: Texas (Culberson County)	F (9)		
27	USA: Texas (El Paso County)	A (1)		
28	USA: Texas (Hudspeth County)	A (2), F (15), T (4)		
29	USA: Texas (Presidio County)	F (16), T (2)		
30	USA: Utah (Washington County)	O (3), Y (9)	Z (4)	AA (1)

museum ($Hd = 0.70$, $\pi = 0.01$) and contemporary samples ($Hd = 0.68$, $\pi = 0.01$). The outlier haplotypes occurred in contemporary samples. Overall, the museum and contemporary samples exhibited genetic structures similar to the full data set, with two large haplogroups separated by ≥7 mutational steps.

Panmixia was rejected by the AMOVA analysis, which showed that substantial genetic variation occurred among populations within groups (30–35%, $\Phi_{SC} = 0.33$–0.36, $P < 0.001$; Table 4). Most genetic variation occurred within populations (62–64%, $\Phi_{ST} = 0.36$–0.39, $P < 0.001$). A statistically significant relationship between geographic distance and genetic distance was revealed by the Mantel test (F_{ST}: $r = 0.42$, $P < 0.001$, $R^2 = 0.179$; Φ_{ST}: $r = 0.35$, $P = 0.002$, $R^2 = 0.120$; Fig. 5).

Unimodal mismatch distributions of both Gambel's Quail haplogroups indicated that each group has undergone recent demographic expansion (Fig. 6). Demographic expansion was further supported by statistically significant and negative values of Fu's F_S (Haplogroups 1 and 2, Table 5).

DISCUSSION

The Gambel's Quail exhibited strong phylogeographic structure as do many arid–adapted taxa of southwestern North America (Riddle et al. 2000, Zink et al. 2001, Zink 2002, Riddle and Hafner 2006). Phylogenetic divergence associated with the Sonoran and Chihuahuan deserts is a frequently observed phenomenon in desert taxa (Riddle and Hafner 2006, Pyron and Burbrink 2010). Deeper, older Chihuahuan–Sonoran diver-

TABLE 4. Analysis of molecular variance results for sampled Gambel's Quail based on different groupings of populations. Shown are degrees of freedom (*df*), sum of squares (*SS*), variance of components (φ), percentage of variance (%), fixation indices (Φ) and *P*-values of the significance of covariance of φ and Φ.

Source of variation	*df*	*SS*	φ	%	Φ	*P*-value
Populations grouped as subspecies						
Among groups	4	44.169	0.213	8.11	$\Phi_{CT} = 0.081$	0.065
Among populations within groups	26	141.819	0.799	30.37	$\Phi_{SC} = 0.331$	<0.001
Within populations	136	220.120	1.619	61.52	$\Phi_{ST} = 0.385$	<0.001
Total	166	406.108	2.631			
Populations grouped geographically						
Among groups	5	56.132	0.029	1.14	$\Phi_{CT} = 0.011$	0.085
Among populations within groups	25	129.856	0.896	35.24	$\Phi_{SC} = 0.356$	<0.001
Within populations	136	220.120	1.619	63.62	$\Phi_{ST} = 0.364$	<0.001
Total	166	406.108	2.544			

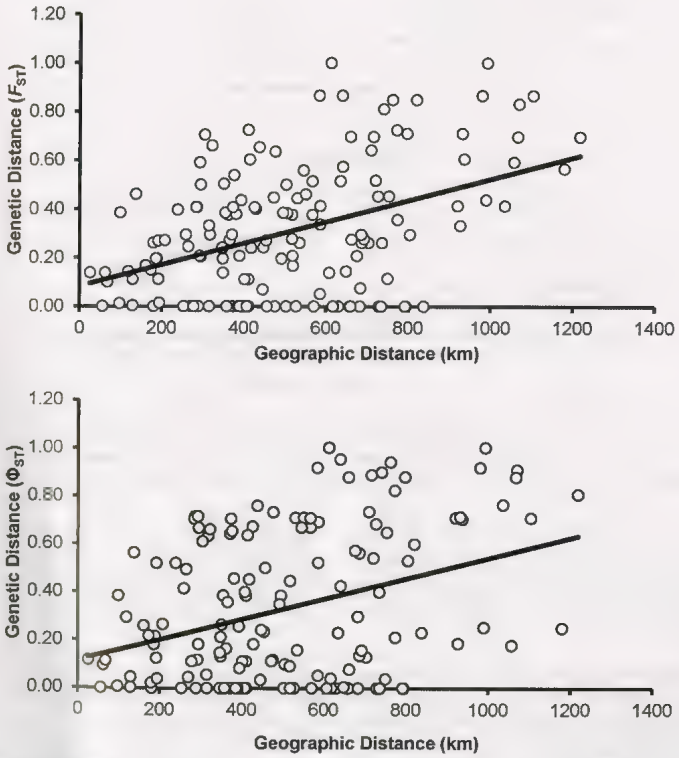


FIG. 5. Mantel test of the degree of genetic isolation of Gambel's Quail based on concatenated mitochondrial control region and ND2 sequences (564 bp) with increasing geographic distance. The y–axis is the genetic distance (either Φ_{ST} or F_{ST}), and the x–axis is the geographic distance in km. Regression equations and coefficients are as follows: Φ_{ST}: $y = 1.219 \times 10^{-3}x - 0.289$; $R^2 = 0.120$; $r = 0.35$, $P < 0.01$; F_{ST}: $y = 1.039 \times 10^{-3}x - 0.223$; $R^2 = 0.179$; $r = 0.42$, $P < 0.001$.

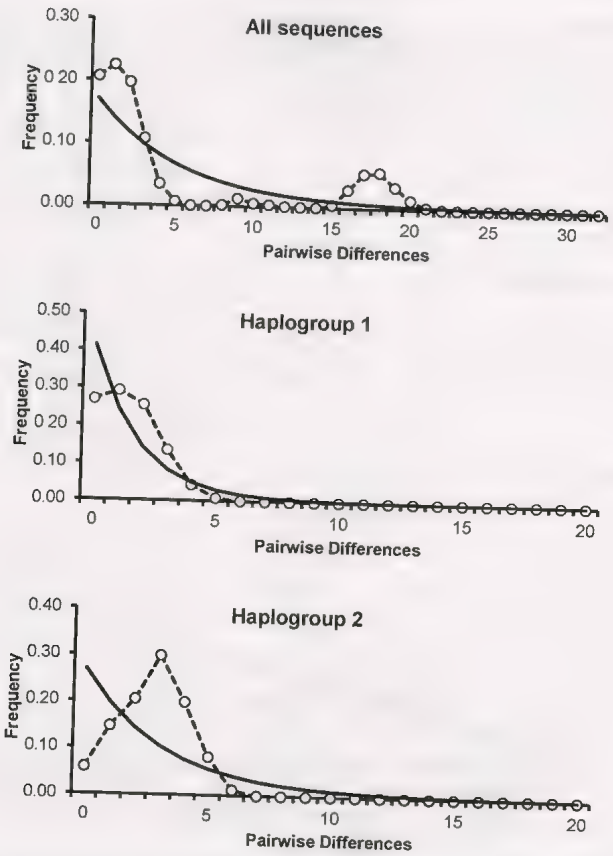


FIG. 6. Observed (solid line) and expected (dashed line) mismatch distributions of the Gambel's Quail (all sequences, $n = 167$) and the two haplogroups, Haplogroups 1 and Haplogroup 2, based on concatenated sequences of the mitochondrial control region and ND2. Mismatch distributions for the two haplogroups excluded outlier haplotypes AA and DD. The x-axis is the number of pairwise differences and the y-axis represents the frequency differences.

gences were probably a result of the Miocene (23.03–5.33 million years ago) uplift of the Sierra Madre Occidental (Riddle 1995, Riddle et al. 2000, Jaeger et al. 2005), whereas, shallower divergences have been attributed to the isolation of populations in separate refugia as a result of Pleistocene climatic oscillations (Riddle and Hafner 2006, Pyron and Burbrink 2010, Bryson et al. 2012).

TABLE 5. Values of mean absolute error (MAE), raggedness (r), and Fu's F_S for the Gambel's Quail and its two haplogroups. Sample size (n) and P-values of raggedness and Fu's F_S are also provided.

	n	S	MAE	r	Fu's F_S
All sequences	167	35	0.741	0.018 ($P = 0.098$)	−12.371 ($P = 0.002$)
Haplogroup 1	146	13	0.438	0.054 ($P = 0.013$)	−14.357 ($P < 0.001$)
Haplogroup 2	19	12	0.803	0.049 ($P = 0.157$)	−7.849 ($P < 0.001$)

Hubbard (1973) hypothesized that the four extant species of *Callipepla* originated when the range of a widespread ancestral species became fragmented during the Illinoian Glaciation (191,000–130,000 years ago). Climate and environmental changes isolated the ancestral species in three separate refugia, including a "pre–*doulgasii*" in Sonora and Sinaloa, "pre–*squamata*" in Chihuahua, and a "pre–*californica/gambelii*" in California (Hubbard 1973, p. 175). The pre–*californica/gambelii* isolate may have expanded into the southwestern United States and northwestern Mexico during the Sangamon Interglacial (125,000–75,000 years ago). During the Wisconsin Glaciation (75,000–19,000 years ago), eastern populations of the pre–*californica/gambelii* isolate became separated in a refugium in the Sonoran Desert, evolving into the modern Gambel's Quail (Hubbard 1973). Zink and Blackwell (1998) estimated that Gambel's and California quails diverged from their common ancestor about 1 million years ago. The genetic break between the haplogroups and outlier haplotypes of the Gambel's Quail are as large as the break between the Haplogroup 1 and California Quail, which suggests that the divergence of these lineages occurred at approximately the same time.

The distribution of the two haplogroups of Gambel's Quail is suggestive of a former Chihuahuan–Sonoran Desert split; however, this inference is obscured by the extensive geographic overlap of the two groups. Secondary contact among divergent Chihuahuan–Sonoran lineages because of post–Pleistocene expansion has been inferred for other non–volant, aridland taxa such as the western diamond-backed rattlesnake (*Crotalus atrox*, Castoe et al. 2007) and the red–spotted toad (*Anaxyrus punctatus*, Jaeger et al. 2005). Admixture observed in the western diamond-backed rattlesnake has resulted from eastward expansion of western lineages (Castoe et al. 2007), and secondary contact among eastern and western lineages of the red–spotted toad has been driven by the westward expansion of eastern lineages from the Chihuahuan Desert (Jaeger et al. 2005). It is not possible to conclusively determine the direction of range expansion of either of the two haplogroups of Gambel's Quail although much of the expansion appears to have been a westward expansion by Haplogroup 1.

Haplotypes AA and DD were genetically differentiated from the main haplogroups, and may be remnants of formerly common lineages. Alternatively, the genetic gaps separating these haplotypes, and the overall genetic structure observed in the Gambel's Quail, may reflect insufficient geographic sampling and sample size. Although the Gambel's and California quails frequently hybridize in parts of southern California where their respective ranges overlap (Grinnell 1915; Johnsgard 1988; Gee 2003, 2004), we detected no obvious evidence of hybridization or mitochondrial introgression among any of the samples. However few Gambel's Quail ($n = 2$) were sampled in this region. The maximum likelihood tree indicated that haplotype AA was the most divergent lineage but clustered with other Gambel's Quail haplotypes although bootstrap support was weak (<50%).

Both haplogroups of Gambel's Quail exhibited star–like phylogenies, with Haplogroup 1 displaying a more typical star network with various haplotypes radiating from a central ancestral haplotype (Fig. 2). Star phylogenies are suggestive of recent, rapid demographic expansions (Slatkin and Hudson 1991), although star–like haplotype networks can also result from population bottlenecks (Depaulis et al. 2003). However, other analyses employed in this study supported demographic expansion as a more plausible explanation. These include the unimodal mismatch distributions, significant, negative values of Fu's F_S, and statistically significant Mantel tests indicating a pattern of isolation by distance, which suggests a geographic gradient of haplotypes potentially caused by range expansion (Excoffier et al. 2009). The lack of large genetic gaps within either haplogroups could indicate that expansion was a relatively recent event. Historically high levels of gene flow among populations may also account for the lack of genetic structure within both haplogroups (Avise 2000).

Assuming that range expansion occurred, how might one explain the events precipitating an expansion of the Gambel's Quail? The expansion of the two haplogroups was most likely driven by climatic changes associated with the end of the Wisconsin Glaciation. Analyses of sediment cores from caves, lakes, and streams (Metcalfe et al. 2002, Pigati et al. 2009, Brook et al. 2006, Chávez–Lara et al. 2012) and pollen and plant macrofossils found in middens constructed by packrats (*Neotoma* spp.; McAuliffe and Van Devender 1998; Metcalfe et al. 2000; Thompson and Anderson 2000; Holmgren et al. 2003, 2011) indicate that the climate of the Chihuahuan and

Sonoran deserts was cooler and wetter during the last glacial period. Cooler, wetter conditions supported open coniferous woodlands in lowlands, while thorn–scrub and shrublands appear to have been absent from the Chihuahuan and Sonoran deserts during the Late Pleistocene (Metcalfe et al. 2000). Modern precipitation regimes and desert shrub communities of southwestern North America were not established until 9,000–4,000 years ago (McAuliffe et al. 1998; Metcalfe et al. 2000; Holmgren et al. 2007, 2011). The distribution of the Gambel's Quail may have been highly restricted during cooler, wetter conditions of the Wisconsin Glaciation. The Gambel's Quail may have undergone rapid expansion during the Holocene as modern desert habitats expanded in southwestern North America. Post–Pleistocene expansions have also been inferred for several desert-adapted animal species (Ayoub and Reichert 2004, Jaeger et al. 2005, Douglas et al. 2006, Castoe et al. 2007, Wilson and Pitts 2012).

The presence of both haplogroups in Sonora, Arizona, Utah–Nevada, and New Mexico–Colorado partly accounts for the high haplotype and nucleotide diversity in these regions, and may represent areas of secondary contact. The higher haplotype and nucleotide diversity in Sonora, Arizona, Utah–Nevada, and New Mexico–Colorado is probably because of the fact this represents the center of the species' range. Western Texas and California–Baja California (where both haplogroups were present) are the respective eastern and western edges of the Gambel's Quails' range, and exhibit the lowest genetic diversity, which is consistent with range expansion, as genetic diversity is usually lower at the edge of a range expansion (Excoffier et al. 2009). Genetic diversity of marginal populations may also be lower because of repeated population crashes caused by suboptimal conditions (Sjörgren 1991), reduced dispersal and immigration (Yamashita and Polis 1995), smaller effective size and genetic drift (Soulé 1973).

The haplogroups identified for Gambel's Quail were not concordant with any of the subspecies, and the AMOVA results suggest that most (>90%) genetic variation occurs among and within populations rather than among subspecies. Our results suggest that the subspecies of Gambel's Quail do not reflect natural groups. The subspecies of Gambel's Quail were based largely on minor variations in plumage coloration and geography (Madge and McGowan 2002) and likely represent sporadic sampling of smooth clinal variation rather than distinct, phenotypically diagnosable units. A lack of concordance between phylogeographic structure and subspecies, however, can result from poor delineation of subspecies boundaries or inaccurate taxonomy (Winker 2010). In fact, many subspecies of North American birds were described on the basis of small samples, individuals collected outside of the breeding season, and non–rigorous descriptions (Rising 2007). For example, Figgins (1913, 1914) argued that Gambel's Quail in southwestern Colorado are descended from Gambel's Quail introduced into Colorado from California in 1885. Mearns (1914) described the subspecies *Callipepla* (*Lophortyx*) *gambelii sana* (*sanus*) on the basis of four specimens from this isolated population that had been provided to the United States National Museum by Figgins (1913). A unique haplotype (JJ) occurred in the single specimen of *C. g. sana* included in this study, but it was embedded within Haplogroup 2 and was most closely related to haplotypes S and BB (haplotypes unique *C. g. gambelii*).

Comparisons of genetic data from historical and contemporary specimens have revealed substantial changes in population structure and diversity in many species as a result of habitat fragmentation, mixing distinct populations, exploitation, or persecution by humans (Roy et al. 1994, Wandeler et al. 2007, Leonard 2008). The difference in the frequency of haplotypes among contemporary and museum specimens suggests that haplotype frequency has changed within ≥100 years. Most museum and contemporary specimens were collected from different localities, which prevented a direct test of changes in haplotype frequencies. The similarity in haplotype and nucleotide diversity among museum and contemporary samples suggests genetic diversity has remained relatively constant for 127 years.

Past attempts to establish game species outside of their native ranges as well as translocations conducted as part of restocking programs are problematic for phylogeographic studies of game species such as Gambel's Quail. Translocations can either obscure or erase the phylogenetic history of populations (Avise 2004). Most attempts at introducing Gambel's Quail outside of their native range have failed (Guillon 1960), with some exceptions such as in Colorado (Figgins 1913, 1914). Tiburón Island populations of the

Gambel's Quail (*C. g. pembertoni*) may also be the result of introductions of this species by humans (Rojas–Soto et al. 2010). Rojas–Soto et al. (2010) found a single ND2 haplotype and two cytochrome *b* (cty*b*) haplotypes among five specimens of *C. g. pembertoni*. The ND2 haplotype and one of the cyt*b* haplotypes was shared by Gambel's Quail from New Mexico, while another cytochrome *b* haplotype was unique to the *C. g. pembertoni* (Rojas–Soto et al. 2010). Similarly, we found only two concatenated ND2–control region haplotypes among three Tiburón Island specimens, but neither of these haplotypes was unique to the island. Human–mediated movements and introductions have also been proposed as explanations for the existence of populations of the California Quail on Santa Catalina Island (Johnson 1972) and populations of Northern Bobwhites on Caribbean Islands (Brennan 1999). Most island populations of New World quails are probably the result of human–mediated introductions, since New World quails are weak fliers, and are largely terrestrial.

It is also possible that selective sweeps or other forms of selection are the cause of the patterns of mtDNA variation we found in Gambel's Quail. The use of mtDNA in phylogeography has been criticized recently because of concerns that selective sweeps may obscure or erase phylogenetic and phylogeographic signals (Ballard and Whitlock 2004, Hurst and Jiggins 2005, Ilves et al. 2010). We cannot conclusively rule out the possibility that selection is responsible for the genetic structure observed, but we consider this to be unlikely for several reasons. First, the Gambel's Quail exhibited a phylogeographic structure similar to other co–distributed desert taxa (Riddle et al. 2000, Zink et al. 2001, Jaeger et al. 2005, Castoe et al. 2007, Wilson et al. 2010). The overall high diversity of mtDNA in natural populations suggests that selective sweeps are rare (Karl et al. 2012), with little evidence that selection has influenced patterns of mtDNA diversity in vertebrates (Nabholz et al. 2008, 2009; McCusker and Bentzen 2010). Selection does not appear to invalidate intraspecific phylogenetic inferences from mtDNA (Zink 2005, Kivisild et al. 2006, Zink et al. 2006). Lastly, numerous phylogeographic studies of birds have reported congruent histories between mitochondrial and nuclear genes (Hung et al. 2013 and references therein), which suggests that mtDNA phylogeographic patterns in most avian species are because of gene flow and genetic drift rather than natural selection (Drovetski et al. 2009; Hung et al. 2012, 2013; Zink et al. 2013).

Although this study suggests little differentiation exists among subspecies of Gambel's Quail, sequence data from *C. g. friedmanni* and *C. g. stephensi* and more intensive sampling of Mexico, California, Nevada, and Colorado will be needed to adequately explore the intraspecific phylogenetics of the Gambel's Quail. Future phylogeographic studies of the Gambel's Quail should include sequences from nuclear loci to evaluate the conclusions of this study, estimate divergence times and effective population size, and provide solid tests of neutrality of mtDNA sequences (Huang et al. 2012, Zink et al. 2013). Finally, a thorough literature review of the original descriptions of all seven subspecies of the Gambel's Quail would also make an important contribution to resolving the species' intraspecific phylogeny (Gutíerrez 1993).

ACKNOWLEDGMENTS

We thank the American Museum of Natural History, University of California–Los Angeles Donald R. Dickey Collection of Birds and Mammals, and the Peabody Museum of Natural History for the use of their museum specimens as sources of genetic material. We thank S. D. Schmenitz, R. Day, D. Olsen of the Utah Division of Wildlife Resources, D. Budeau of the Oregon Department of Fish and Wildlife, J. McCanna of the Washington State Department of Fish and Wildlife, and numerous local hunters for their assistance in collecting contemporary samples of Gambel's and California Quail. We thank A. Zamorano Arreola, K. Corman, and J. Sumners for assistance in the laboratory. Laboratory facilities were greatly enhanced by gifts from the Lawrence Family Foundation and the Caesar Kleberg Foundation. J. Sands, W. Kuvlesky, and two anonymous referees provided helpful reviews of this manuscript. Funding for this project was provided by the Elliot B. and Adelle Bottom Fellowship in Quail Research and the South Texas Quail Associates. The C. C. Winn Endowed Chair supported L. A. Brennan and the Alfred C. Glassell, Jr. Endowed Professorship supported F. Hernández. This is Caesar Kleberg Wildlife Research Institute Publication Number 13–115.

LITERATURE CITED

AKAIKE, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

AVISE, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts, USA.

AVISE, J. C. 2004. Molecular markers, natural history, and evolution. Second Edition. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

AYOUB, N. A. AND S. E. RIECHERT. 2004. Molecular evidence for Pleistocene glacial cycles driving diversification of a North American desert spider, *Agelenopsis aperta*. Molecular Ecology 13:3453–3465.

BALLARD, J. W. O. AND M. C. WHITLOCK. 2004. The incomplete natural history of mitochondria. Molecular Ecology 13:729–744.

BARROWCLOUGH, G. F. AND R. M. ZINK. 2009. Funds enough, and time: mtDNA, nuDNA and the discovery of divergence. Molecular Ecology 18:2934–2936.

BRENNAN, L. A. 1999. Northern Bobwhite (*Colinus virginianus*). The birds of North America. Number 397.

BROOK, G. A., B. B. ELLWOOD, L. B. RAILSBACK, AND J. B. COWART. 2006. A 164 ka record of environmental change in the American Southwest from a Carlsbad Cavern speleothem. Palaeogeography, Palaeoclimatology, Palaeoecology 237:483–507.

BROWN, D. E., J. C. HAMELIN, M. TAYLOR, AND J. GALLOWAY. 1998. Gambel's Quail (*Callipepla gambelii*). The birds of North America. Number 321.

CASTOE, T. A., C. L. SPENCER, AND C. L. PARKINSON. 2007. Phylogeographic structure and historical demography of the western diamondback rattlesnake (*Crotalus atrox*): a perspective on North American desert biogeography. Molecular Phylogenetics and Evolution 42:193–212.

CHÁVEZ–LARA, C. M., P. D. ROY, M. M. CABALLERO, A. L. CARREÑO, AND C. LAKSHUMANAN. 2012. Lacustrine ostracodes from the Chihuahuan Desert of Mexico and inferred Late Quaternary paleoecological conditions. Revista Mexicana de Ciencias Geológicas 29:422–431.

DARRIBA, D., G. L. TABOADA, R. DOALLO, AND D. POSADA. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772.

DEPAULIS, F., S. MOUSSET, AND M. VEUILLE. 2003. Power of neutrality tests to detect bottlenecks and hitchhiking. Journal of Molecular Evolution 57:S190–S200.

DOUGLAS, M. E., M. R. DOUGLAS, G. W. SCHUETT, AND L. W. PORRAS. 2006. Evolution of rattlesnakes (Viperidae; *Crotalus*) in the warm deserts of western North America shaped by Neogene vicariance and Quaternary climate change. Molecular Ecology 15:3353–3374.

DROVETSKI, S. V., R. M. ZINK, AND N. A. MODE. 2009. Patchy distributions belie morphological and genetic homogeneity in rosy–finches. Molecular Phylogenetics and Evolution 50:437–445.

EXCOFFIER, L., M. FOLL, AND R. J. PETIT. 2009. Genetic consequences of range expansions. Annual Reviews in Ecology, Evolution, and Systematics 40:481–501.

EXCOFFIER, L. AND H. E. L. LISCHER. 2010. ARLEQUIN suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10:564–567.

EXCOFFIER, L. AND P. E. SMOUSE. 1994. Using allele frequencies and geographic subdivision to reconstruct trees within a species: molecular variance parsimony. Genetics 136:343–359.

EXCOFFIER, L., P. SMOUSE, AND J. QUATTRO. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

FIGGINS, J. D. 1913. The status of the Gambel's Quail in Colorado. Condor 15:158.

FIGGINS, J. D. 1914. The fallacy of the tendency towards ultraminute distinctions. Auk 31:62–69.

FU, Y.-X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925.

GEE, J. M. 2003. How a hybrid zone is maintained: behavioral mechanisms of interbreeding between California and Gambel's quail (*Callipepla californica* and *C. gambelii*). Evolution 57:2407–2415.

GEE, J. M. 2004. Gene flow across a climatic barrier between hybridizing avian species, California and Gambel's quail (*Callipepla californica* and *C. gambelii*). Evolution 58:1108–1121.

GRINNELL, J. 1915. A distributional list of the birds of California. Pacific Coast Avifauna 2:1–217.

GUILLON, G. W. 1960. The ecology of Gambel's Quail in Nevada and the arid southwest. Ecology 41:518–536.

GUINDON, S. AND O. GAUSCEL. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52:696–704.

GUTIÉRREZ, R. J. 1993. Taxonomy and biogeography of New World quail. Proceedings of the National Quail Symposium 3:8–15.

GUTIÉRREZ, R. J., R. M. ZINK, AND S. Y. YANG. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. Auk 100:33–47.

HACKETT, S. J. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Molecular Phylogenetics and Evolution 5:368–382.

HARRISON, S. AND A. HASTINGS. 1996. Genetic and evolutionary consequences of metapopulation structure. Trends in Ecology and Evolution 11:180–183.

HARPENDING, H. C. 1994. Signature of ancient population growth in a low–resolution mitochondrial mismatch distribution. Human Biology 66:591–600.

HASEGAWA, M. H. KISHINO, AND T. YANO. 1985. Dating the human–ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22:160–174.

HELLMAYR, C. E. AND B. CONOVER. 1942. Catalogue of birds of the Americas and adjacent islands. Field Museum of Natural History Zoological Series. Number 13.

HOLMAN, J. A. 1961. Osteology of living and fossil New World quails (Aves, Galliformes). Bulletin of the Florida State Museum, Biological Sciences 6:131–233.

HOLMGREN, C. A., J. NORRIS, AND J. L. BETANCOURT. 2007. Inferences about winter temperatures and summer rains from the late Quaternary record of C_4 perennial grasses and C_3 desert shrubs in the northern Chihuahuan Desert. Journal of Quaternary Science 22:141–161.

HOLMGREN, C. A., M. C. PEÑLBA, K. A. RYLANDER, AND J. L. BETANCOURT. 2003. A 16,000 ^{14}C yr B.P. packrat

midden series from the USA–Mexico borderlands. Quaternary Research 60:319–329.

HOLMGREN, C. A., J. L. BETANCOURT, AND K. A. RYLANDER. 2011. Vegetation history along the eastern, desert escarpment of the Sierra San Pedro Martír, Baja California, Mexico. Quaternary Research 75:647–657.

HUBBARD, J. P. 1973. Avian evolution in the aridlands of North America. Living Bird 12:155–196.

HUDSON, R. R. 1990. Gene genealogies and the coalescent process. Oxford Surveys in Evolutionary Biology 7:1–44.

HUMMEL, S. 2003. Ancient DNA typing. Springer, New York, USA.

HUNG, C.-M., S. V. DROVETSKI, AND R. M. ZINK. 2012. Multilocus coalescence analyses support a mtDNA–based phylogeographic history for a widespread Palearctic passerine bird, *Sitta europaea*. Evolution 66:2850–2864.

HUNG, C.-M., S. V. DROVETSKI, AND R. M. ZINK. 2013. Multilocus test of the absence of mtDNA phylogeographic structure in a widespread wader, the Common Sandpiper (*Actitis hypoleucos*). Journal of Ornithology 154:1105–1113.

HURST, G. D. D. AND F. M. JIGGINS. 2005. Problems with mitochondrial DNA as a marker in population, phylogeographic and phylogenetic studies: the effects of inherited symbionts. Proceedings of the Royal Society of London, Series B 272:1525–1534.

ILVES, K. L., W. HUANG, J. P. WARES, AND M. J. HICKERSON. 2010. Colonization and/or mitochondrial selective sweeps across the North Atlantic intertidal assemblage revealed by multi–taxa approximate Bayesian computation. Molecular Ecology 19:4505–4519.

JAEGER, J. R., B. R. RIDDLE, AND D. F. BRADFORD. 2005. Cryptic neogene vicariance and Quaternary dispersal of the red–spotted toad (*Bufo punctatus*): insights on the evolution of North American warm desert biotas. Molecular Ecology 14:3033–3048.

JENSEN, J. L., A. J. BOHANAK, AND S. T. KELLEY. 2005. Isolation by distance, web service. BMC Genetics 6:13.

JOHNSGARD, P. A. 1988. The quails, partridges, and francolins of the world. Oxford University Press, UK.

JOHNSON, N. K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. Condor 74:295–315.

KARL, S. A., R. J. TOONEN, W. S. GRANT, AND B. W. BOWEN. 2012. Common misconceptions in molecular ecology: echos of the modern synthesis. Molecular Ecology 21:4171–4189.

KIVISILD, T., P. SHEN, D. P. WALL, B. DO, R. SUNG, K. DAVIS, G. PASSARINO, P. A. UNDERHILL, C. SCHARFE, A. TORRONI, R. SCOZZARI, D. MODIANO, A. COPPA, P. DE KNIJFF, M. FELDMAN, L. L. CAVALLI–SFORZA, AND P. J. OEFNER. 2006. The role of selection in the evolution of human mitochondrial genomes. Genetics 172:373–387.

KRUSKAL, J. B. 1956. On the shortest spanning subtree of a graph and the travelling salesman problem. Proceedings of the American Mathematics Society 7:48–50.

LARKIN, M. A., G. BLACKSHIELDS, N. P. BROWN, R. CHENNA, P. A. MCGETTIGAN, H. MCWILLIAM, F. VELENTIN, I. M. WALLACE, A. WILM, R. LOPEZ, J. D. THOMPSON, T. J. GIBSON, AND D. G. HIGGINS. 2007. CLUSTAL W and CLUSTAL X Version 2.0. Bioinformatics 23:2947–2948.

LEONARD, J. A. 2008. Ancient DNA applications for wildlife conservation. Molecular Ecology 17:4186–4196.

LIBRADO, P. AND J. ROZAS. 2009. DNASP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25:1451–1452.

MADGE, S. AND P. MCGOWAN. 2002. Pheasants, partridges, and grouse: a guide to the pheasants, partridges, quails, grouse, guineafowl, buttonquails, and sandgrouse of the world. Princeton University Press, New Jersey, USA.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209–220.

MCAULIFFE, J. R. AND T. R. VAN DEVENDER. 1998. A 22,000–year record of vegetation change in the north–central Sonoran Desert. Palaeogeography, Palaeoclimatology, Palaeoecology 141:253–275.

MCCUSKER, M. R. AND P. BENTZEN. 2010. Positive relationships between genetic diversity and abundance in fishes. Molecular Ecology 19:4852–4862.

MEARNS, E. A. 1914. Diagnosis of a new subspecies of Gambel's Quail from Colorado. Proceedings of the Biological Society of Washington 27:113.

METCALFE, S. E., S. L. O'HARA, M. CABALLERO, AND S. J. DAVIES. 2000. Records of Late Pleistocene–Holocene climatic change in Mexico — a review. Quaternary Science Reviews 19:699–721.

METCALFE, S., A. SAY, S. BLACK, R. MCCULLOCH, AND S. O'HARA. 2002. Wet conditions during the last glaciation in the Chihuahuan Desert, Alta Babicora Basin, Mexico. Quaternary Research 57:91–101.

MULLIGAN, C. J. 2005. Isolation and analysis of DNA from archaeological, clinical, and natural history specimens. Methods in Enzymology 395:87–103.

MUNDY, N. I., P. UNITT, AND D. S. WOODRUFF. 1997. Skin from the feet of museum specimens as a non–destructive sources of DNA for avian genotyping. Auk 114:126–129.

NABHOLZ, B., S. GLÉMIN, AND N. GALTIER. 2009. The erratic mitochondrial clock: variations of mutation rate, not population size, affect mtDNA diversity across birds and mammals. BMC Evolutionary Biology 9:54.

NABHOLZ, B., J.–F. MAUFFREY, E. BAZIN, N. GALTIER, AND S. GLEMIN. 2008. Determination of mitochondrial genetic diversity in mammals. Genetics 178:351–361.

NEDBAL, M. A., R. L. HONEYCUTT, S. G. EVANS, R. M. WHITING, AND D. R. DIETZ. 1997. Northern Bobwhite restocking in east Texas: a genetic assessment. Journal of Wildlife Management 61:854–863.

NEI, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, USA.

NGAN, E. C. 2006. Isolation by distance web service with incorporation of DNA data sets. Thesis. San Diego State University, California, USA.

OMLAND, K. E., S. M. LANYON, AND S. J. FRITZ. 1999. A molecular phylogeny of the New World orioles (*Icterus*): the importance of dense taxon sampling. Molecular Phylogenetics and Evolution 12:224–239.

PÄÄBO, S., H. POINAR, D. SERRE, V. JAENICKE–DESPRÉS, J. HEBLER, N. ROHLAND, M. KUCH, J. KRAUSE, L. VIGILANT, AND M. HOFREITER. 2004. Genetic analyses from ancient DNA. Annual Review of Genetics 38:645–679.

PEAKALL, R. AND P. E. SMOUSE. 2006. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research–an update. Bioinformatics 28:2537–2539.

PIGATI, J. S., J. E. BRIGHT, T. M. SHANAHAN, AND S. A. MAHAN. 2009. Late Pleistocene paleohydrology near the boundary of the Sonoran and Chihuahuan Deserts, southeastern Arizona. Quaternary Science Reviews 28:286–300.

PITELKA, F. A. 1948. Notes on the distribution and taxonomy of Mexican game birds. Condor 50:113–123.

PRESS, W. H., S. A. TEUKOLSKY, W. T. VETTERLING, AND B. P. FLANNERY. 1992. Numerical recipes in C. The art of computing. Cambridge University Press, UK.

PRIM, R. C. 1957. Shortest connection networks and some generalizations. Bell Systems Technical Journal 36:1389–1401.

PYRON, R. A. AND F. T. BURBRINK. 2010. Hard and soft allopatry: physically and ecologically mediated modes of geographic speciation. Journal of Biogeography 37:2005–2015.

RAMÍREZ–SORIANO, A., S. E. RAMOS–ONSINS, J. ROZAS, F. CALAFELL, AND A. NAVARRO. 2008. Statistical power analysis of neutrality tests under demographic expansions, contractions and bottlenecks with recombination. Genetics 179:555–567.

RAMOS–ONSINS, S. E. AND J. ROZAS. 2002. Statistical properties of new neutrality test against population growth. Molecular Biology and Evolution 19:2092–2100.

RIDDLE, B. R. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): the late Cenozoic development of a North American aridlands rodent guild. Journal of Mammalogy 76:283–301.

RIDDLE, B. R. AND D. J. HAFNER. 2006. A step–wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. Journal of Arid Environments 66:435–461.

RIDDLE, B. R., D. J. HAFNER, AND L. F. ALEXANDER. 2000. Phylogeography and systematics of the *Peromyscus eremicus* species group and the historical biogeography of North American warm regional deserts. Molecular Phylogenetics and Evolution 17:145–160.

RIDDLE, B. R., D. J. HAFNER, L. F. ALEXANDER, AND J. R. JAEGER. 2000. Cryptic vicariance in the historical assembly of a Baja California peninsular desert biota. Proceedings of the National Academy of Science of the USA 97:14483–14443.

RISING, J. D. 2007. Named subspecies and their significance in contemporary ornithology. Ornithological Monographs 63:45–54.

RIDGELY, R. S., T. F. ALLNUTT, T. BROOKS, D. K. MCNICOL, D. W. MEHLMAN, B. E. YOUNG, AND J. R. ZOOK. 2007. Digital distribution maps of the birds of the Western Hemisphere, Version 3.0. NatureServe. http://www.natureserve.org (accessed 5 Oct 2012).

RIDGWAY, R. AND H. FRIEDMANN. 1946. The birds of North and Middle America. U.S. National Museum Bulletin. Number 50.

ROGERS, A. R. AND H. HARPENDING. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Molecular Biology and Evolution 9:552–569.

ROHLF, F. J. 1973. Algorithm 76. Hierarchical clustering using the minimum spanning tree. Computer Journal 16:93–95.

ROJAS–SOTO, O. R., M. WESTBURG, A. G. NAVARRO–SIGÜENZA, AND R. M. ZINK. 2010. Genetic and ecological differentiation in the endemic avifauna of Tiburón Island. Journal of Avian Biology 41:398–406.

ROY, M. S., D. J. GIRMAN, A. C. TAYLOR, AND R. K. WAYNE. 1994. The use of museum specimens to reconstruct the genetic variability and relationships of extinct populations. Experientia 50:551–557.

SINNOTT, R. W. 1984. Virtues of the haversine. Sky and Telescope 68:159.

SJÖRGREN, P. 1991. Genetic variation in relation to demography of peripheral pool frog populations (*Rana lessonae*). Evolutionary Ecology 5:248–271.

SLATKIN, M. AND R. R. HUDSON. 1991. Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics 129:555–562.

SOULÉ, M. 1973. The epistasis cycle: a theory of marginal populations. Annual Review of Ecology and Systematics 4:165–187.

SULLINS, M. R. 2006. Diet composition and distribution of Gambel's Quail in the Trans–Pecos. Thesis. Sul Ross University, Alpine, Texas, USA.

TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI, AND S. KUMAR. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony. Molecular Biology and Evolution 28:2731–2739.

TEACHER, A. G. F. AND D. J. GRIFFITHS. 2011. HAPSTAR: automated haplotype network layout and visualization. Molecular Ecology Resources 11:151–153.

TEXAS GAME, FISH AND OYSTER COMMISSION. 1945. Principal game birds and mammals of Texas. Texas Game, Fish and Oyster Commission, Austin, Texas, USA.

THOMPSON, R. S. AND K. H. ANDERSON. 2000. Biomes of western North America at 18,000, 6000 and 0 ^{14}C yr BP reconstructed from pollen and packrat midden data. Journal of Biogeography 27:555–584.

VAIDYA, G., D. J. LOHMAN, AND R. MEIER. 2011. SEQUENCEMATRIX: concatenation software for the fast assembly of gene dataset and codon information. Cladistics 27:171–180.

VAN DEN BUSSCHE, R. A., S. R. HOOFER, D. A. WIEDNFELD, D. H. WOLFE, AND S. D. SHERROD. 2003. Genetic variation within and among fragmented

populations of Lesser Prairie–Chickens (*Tympanuchus pallidicintus*). Molecular Ecology 12:675–683.

VIGILANT, L., M. STONEKING, H. C. HARPENDING, K. HAWKES, AND A. C. WILSON. 1991. African populations and the evolution of human mitochondrial DNA. Science 253:1503–1507.

WANDELER, P., P. E. A. HOECK, AND L. F. KELLER. 2007. Back to the future: museum specimens in population genetics. Trends in Ecology and Evolution 22:634–642.

WATTERSON, G. A. 1975. On the number of segregating sites in genetical models without recombination. Theoretical Population Biology 7: 256–276.

WENINK, P. W., A. J. BAKER, AND M. G. TILANUS. 1994. Mitochondrial control–region sequences in two shorebird species, the turnstone and the dunlin, and their utility in population genetic studies. Molecular Biology and Evolution 11:22–31.

WILSON, J. S. AND J. P. PITTS. 2012. Identifying Pleistocene refugia in North American cold deserts using phylogeographic analyses and ecological nigh modeling. Diversity and Distributions 18:1139–1152.

WILSON, J. S., K. A. WILLIAMS, C. F. GUNNELL, AND J. P. PITTS. 2010. Phylogeographic investigations of the widespread, arid–adapted antlion *Brachynemurus sackeni* Hagen (Neuroptera: Myrmeleontidae). Psyche 2010:804709.

WINKER, K. 2010. Subspecies represent geographically partitioned variation, a gold mine of evolutionary biology, and a challenge for conservation. Ornithological Monographs 67:6–23.

YAMASHITA, T. AND G. A. POLIS. 1995. A test of the central–marginal model using sand scorpion populations (*Paruroctonus mesaensis*, Vaejovidae). Journal of Arachnology 23:60–64.

ZINK, R. M. 2002. Methods in comparative phylogeography, and their application to studying evolution in the North American aridlands. Integrative Comparative Biology 42:953–959.

ZINK, R. M. 2005. Natural selection on mitochondrial DNA in *Parus* and its relevance for phylogeographic studies. Proceedings of the Royal Society of London, Series B 272:71–78.

ZINK, R. M. AND G. F. BARROWCLOUGH. 2008. Mitochondrial DNA under siege in avian phylogeography. Molecular Ecology 17:2107–2121.

ZINK, R. M. AND R. C. BLACKWELL. 1998. Molecular systematics of the Scaled Quail complex (genus *Callipepla*). Auk 115:394–403.

ZINK, R. M., S. V. DROVETSKI, AND S. ROHWER. 2006. Selective neutrality of mitochondrial ND2 sequences, phylogeography and species limits in *Sitta europaea*. Molecular Phylogenetics and Evolution 40:679–686.

ZINK, R. M., J. G. GROTH, H. VÁZQUEZ–MIRANDA, AND G. F. BARROWCLOUGH. 2013. Phylogeography of the California Gnatcatcher (*Polioptila californica*) using multilocus DNA sequences and ecological niche modeling: implications for conservation. Auk 130:449–458.

ZINK, R. M., A. E. KESSEN, T. V. LINE, AND R. C. BLACKWELL–RAGO. 2001. Comparative phylogeography of some aridland bird species. Condor 103:1–10.

ZINK, R. M., D. F. LOTT, AND D. W. ANDERSON. 1987. Genetic variation, population structure, and evolution of California Quail. Condor 89:395–405.

The Wilson Journal of Ornithology 126(2):236–248, 2014

RANGE EXPANSION AND THE BREAKDOWN OF BERGMANN'S RULE IN RED-BELLIED WOODPECKERS (*MELANERPES CAROLINUS*)

JEREMY J. KIRCHMAN[1,3] AND KATHRYN J. SCHNEIDER[2]

ABSTRACT.—Previous studies of northward expansion of breeding ranges of North American bird species have focused on correlated changes in climate and land-use, but very few studies have examined patterns of morphological change within the context of range expansion. We used data from museum specimens to examine geographic and temporal variation in body size of the Red-bellied Woodpecker (*Melanerpes carolinus*), a species undergoing dramatic range expansion. We plotted georeferenced occurrence data from Christmas Bird Counts (winter distributions going back to the year 1900), USGS Breeding Bird Surveys (summer distributions since 1966), and the holdings of twenty-six natural history museums (year-round distributions since 1867) to document the historic range of *M. carolinus* in decade increments. Christmas Bird Counts, but not museum specimens, indicate a trend of slow northward expansion beginning as early as the 1910s, and all data sets show rapid expansion to the north and west since the 1950s (average of 0.85° N latitude per decade and 1.06° W longitude per decade). Geographic variation in body size of specimens collected prior to the period of rapid expansion follows Bergmann's rule, with larger birds occurring in northern latitudes. This pattern breaks down in the sample of birds collected after the onset of rapid expansion, suggesting that warming temperatures since the 1950s have enabled northward range expansion in a species previously limited by cold. Birds collected at the northern boundary of their range before 1940 were larger than birds collected in recent decades from the same latitudes, further supporting the hypothesis that Red-bellied Woodpeckers have been released from a former ecological or physiological constraint in the face of climate warming. *Received 31 May 2013. Accepted 20 December 2013.*

Key words: Bergmann's rule, Breeding Bird Survey, Christmas Bird Count, climate change, geographic variation, range expansion, Red-bellied Woodpecker.

Long-term data sets documenting bird distributions reveal decade-scale dynamics in the ranges of many species. Museum specimen collections and repeated scientific surveys (e.g., Tingley et al. 2009), as well as data from citizen-science projects such as repeated state breeding bird atlases, the Cornell Lab of Ornithology's Project Feeder Watch, National Audubon Society's Christmas Bird Count and the USGS Breeding Bird Survey, have been used to examine the patterns and potential causes of range shifts in birds (Root and Weckstein 1994; Hitch and Leberg 2007; Mehlman 1997; LaSorte and Thompson 2007; Zuckerburg et al. 2009, 2011). The majority of range shifts in diverse species assemblages are consistent with expected response to recent climate warming (Parmesan and Yohe 2003, Root et al. 2003), but some species have moved in the opposite direction and many species have not moved at all (McGowan and Zuckerberg 2008). The northward expansion of some elements of the "Carolinian avifauna" is a particularly compelling case of range shift in the face of climate warming. Northward movement of several presumably cold-limited species endemic to the southeastern United States has long been recognized (Beddall 1963, Robinson 1977, Kricher 1981, Stiles 1982, David et al. 1990, Ellison 1993, Jackson and Davis 1998). But whereas several studies have found that latitudinal and altitudinal range shifts can be explained by models that include climate variables, changes in land use, habitat structure, bird feeding, and interspecific competition are also important drivers of distributional changes in birds (Emlen et al. 1986, Root and Weckstein 1994, Hitch and Leberg 2007, Zuckerberg et al. 2009, Zuckerberg et al. 2011).

Distribution shifts are interesting, because they provide insights regarding the ecological and evolutionary factors that limit species ranges (Holt 2003). Root (1988a,b) found that the northern range boundaries of 148 bird species wintering in the United States were strongly associated with average minimum January temperature and that the northern limits of many species' ranges were restricted by metabolic rate. Selection for cold tolerance, in addition to determining range limits, is the likely basis for latitudinal clines in body size within species such as in Bergmann's rule, the observation that larger

[1] New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, USA.

[2] Department of Biology, Chemistry and Physics, Hudson Valley Community College, 80 Vandenburgh Avenue, Troy, NY 12180, USA.

[3] Corresponding author; e-mail: jkirchma@mail.nysed.gov

individuals are found in colder regions in geographically widespread species of birds and mammals (Bergmann 1847, James 1970). As organisms increase in size, they grow more rapidly in volume than surface area. Because heat loss depends on surface area, large animals with a smaller surface to volume ratio will be at an advantage in colder climates. The generality of Bergmann's rule has been disputed (Meiri et al. 2009), but Meiri and Dayan (2003) found it to be the pervasive pattern of geographic variation in a sample of 94 bird species, and Zink and Remsen (1986) and James (1970) showed that it fits the morphological patterns observed in many non-migratory bird species, and is especially prevalent in woodpeckers. Ramirez et al. (2008) used published and estimated mean body masses for >3800 bird species from North and South America to confirm that birds (species in this case, not individuals) are larger closer to the poles, and that the trend is stronger in winter than in summer because of seasonal range shifts of migratory species. They concluded that winter temperatures drive the latitudinal gradient of body size in birds.

The link between climate and body size in birds has led some researchers to investigate changes in body size over recent decades. McCoy (2012) measured museum specimens collected in Connecticut before and after the onset of rapidly warming temperatures (defined in that paper as 1955), and found significant reductions in wing length (a proxy for body size) over time in three species (Purple Finch *Haemorhous purpureus*, Blue Jay *Cyanocitta cristata*, and Common Grackle *Quiscalus quiscula*). Yom-Tov et al. (2006) found reductions in body weight of four species banded in England over a 30-year period, and Van Buskirk et al. (2010) found steady reductions in mass and wing-chord over a 45-year period for several species captured at a migration monitoring station in Pennsylvania. In these studies, declining body size was interpreted as evidence of weakening selection on body size because of climate warming. The trend of shrinking body size with climate warming at one geographic locality is consistent with predictions based on Bergmann's rule, but no study has examined recent changes in body size variation across latitude, or investigated how range dynamics might alter geographic patterns of body size or other morphological characters under apparent selection for cold-tolerance.

In this study we ask whether the period of northward range expansion by Carolinean bird species has been accompanied by morphological change consistent with easing of selection for cold-tolerance. To address this question we simultaneously examined range dynamics and morphological evolution of the Red-bellied Woodpecker (*Melanerpes carolinus*) in North America on decade to century time scales using three long term data sets: National Audubon Society North American Christmas Bird Counts (CBC), United States Geological Survey Breeding Bird Surveys (BBS), and specimen data from North American natural history museums. Red-bellied Woodpeckers are non-migratory and are currently considered monotypic (Short 1982, Shackelford et al. 2000), although four subspecies were recognized by the American Ornithologists' Union (AOU; 1957) based on the work of Burleigh and Lowery (1944) and Koelz (1954). These authors focused mostly on plumage differences but geographic variability in bill length and wing length is known to occur. Males average slightly larger than females, but Pyle (1997) describes the variation as "broadly clinal and obscured by individual variation." Jackson and Davis (1998) suggested that range expansion in Red-bellied Woodpeckers began in the early 1900s, the result of a combination of reforestation, Dutch elm disease, climate change, and bird feeding. Emlen et al. (1986) identified latitude as the single most important environmental correlate of density of Red-bellied Woodpeckers surveyed along a latitudinal transect in the bottomland forests of the Mississippi River valley. The study by Zuckerberg et al. (2009) concluded that Red-bellied Woodpeckers were among the most climate restricted species, being strongly limited by the average minimum temperature throughout a winter season. Their analysis of winter-long changes in site occupancy also showed that Red-bellied Woodpeckers had a higher probability of extirpation at colder sites even though they regularly visited supplemental food sources.

We plotted occurrence data to document the historic range of the Red-bellied Woodpecker in decade increments. We then measured museum specimens collected throughout the species' range both before and after the onset of northward expansion. Our goals were to measure as many study skins as possible from newly colonized areas to see if the "pioneers" had physical characteristics that were different from others in

TABLE 1. Museum holdings of specimens used to document historical occurrence of Red-bellied Woodpeckers. Institutions marked with * provided access to or loans of specimens used in morphological analyses.

Institution	Location	Approximate number of specimens
American Museum of Natural History*	New York, NY	227
Academy of Natural Sciences	Philadelphia, PA	87
Bell Museum of Natural History*	Minneapolis, MN	35
Columbia Greene Community College*	Hudson, NY	9
Carnegie Museum of Natural History*	Pittsburg, PA	83
Canadian Museum of Nature*	Ottawa, ON	12
Cleveland Museum of Natural History	Cleveland, OH	42
Cornell Museum of Vertebrates*	Ithaca, NY	66
Delaware Museum of Natural History*	Wilmington, DE	38
Denver Museum of Natural Science*	Denver, CO	32
Field Museum of Natural History*	Chicago, IL	317
Illinois State University	Normal, IL	12
University of Kansas*	Lawrence, KS	171
Museum of Comparative Zoology*	Cambridge, MA	352
Michigan State University Museum	Lansing, MI	15
New York State Museum*	Albany, NY	16
Royal Ontario Museum	Toronto, ON	88
Sam Noble Museum of Natural History*	Norman, OK	174
University of Michigan Museum of Zoology*	Ann Arbor, MI	183
University of Nebraska State Museum*	Lincoln, NE	15
US National Museum, Smithsonian Institution	Washington, DC	516
Yale Peabody Museum*	New Haven, CT	30

the population and to see if the recent colonization of more northern latitudes was accompanied by changes in body size. Climatological data clearly show that winter temperatures have risen steadily in North America (Intergovernmenatl Panel on Climate Change 2007). If temperature constraints influence body size, we would expect birds collected in recent decades, now freed from the restrictions of a cold climate, to be smaller than birds that occupied northern borders of the species range during colder times.

METHODS

In August–September 2010, we obtained occurrence records of *M. carolinus* by requesting data from the National Audubon Society for the North American Christmas Bird Count (CBC), the United States Geological Survey for the Breeding Bird Survey (BBS), and from North American natural history museums by searching the ORNIS data portal (www.ornisnet.org) and contacting museum curators and collections managers. For CBC data, we requested localities for all CBC "circles" and for all CBCs reporting at least one *M. carolinus* from the program's inception in 1900 to the present. Latitude and longitude correspond to the center of each 24-km diameter count circle. BBS data comprised all routes surveyed and all routes reporting at least one *M. carolinus* from the program's inception in 1966 to the present, with latitude and longitude corresponding to the start of the 40.23-km route. Not every CBC circle or BBS route was counted every year, and some were added over time while others were discontinued. In order to map the species' winter range (CBC) and summer range (BBS) over time, we pooled the data by decade, identifying and plotting any CBC circle or BBS route where *M. carolinus* was observed at least once during the decade. Over the 110+ year history of the CBC and the 40+ years of the BBS, these decade-long windows summarize *M. carolinus* sightings from 40 states, the District of Columbia and eight Canadian provinces.

We used ORNIS, searchable museum websites, and data provided by curators to compile date and locality information on more than 2,500 *M. carolinus* specimens held in the collections shown in Table 1. We did not include specimen records for which year of collection was not recorded, or for which locality information was less precise than county. Some museums (especially CMN, DMNS, FMNH, NYSM, ROM, UMMZ, YPM, listed in Table 1) provided latitude and longitude

data for some or all of their specimens. For specimens without coordinate information we used GEOLocate version 3.22 (www.museum.tulane.edu/geolocate.html), BioGeomancer (Guralnick et al. 2006), or MaNIS Georeferencing Calculator (manisnet.org/gci2.html) to georeference the localities according to MaNIS/HerpNET/ORNIS Guidelines (Wieczorek et al. 2004, Chapman and Wieczorek 2006). In general we used GEOLocate if the locality was a place name, a street address or had single orthogonal offsets. If the locality was a county, we used BioGeomancer. For localities with two orthogonal offsets we used MaNIS Georeferencing Calculator. We were unable to georeference about 8% of museum specimens because of imprecise verbal locality descriptions, leaving us with 1997 specimens with useful date and locality information.

We plotted occurrences from all three data sets using Arc Map version 9.3. These maps allowed us to estimate the boundaries of the Red-bellied Woodpecker's summer and winter ranges for each decade. Plotting all CBC circles and BBS routes surveyed at least once each decade allowed us to verify that these survey programs had sufficient geographic coverage to delimit the boundaries of the species' range. We quantified the movement of the northern boundaries of the range over time in all three data sets by calculating the mean and standard deviation of the latitude of the ten northern-most occurrences in each decade and the most northern 5% of occurrences in each decade. We tracked movement of the western boundary in the same way using longitudes of the ten western-most occurrences and the most western 5% of occurrences in each decade. The southern and eastern boundaries were constrained by the Gulf of Mexico and Atlantic Ocean.

Although we were especially interested in measuring birds at the edge of the range and "pioneers" collected from the expanding front, we endeavored to measure adult individuals of both sexes throughout their range from all time periods to provide baseline estimates of geographic variation in body size and shape. We visited or received loans of specimens from the museums listed in Table 1 and measured a total of 406 study skins. Using digital calipers we took five measurements on each bird to the nearest 0.1 mm: 1) length of unflattened wing chord from the carpal joint of the right wing to the distal end of the outermost primary, 2) length of wing from the carpal joint of the right wing to the distal end of the outermost secondary, 3) exposed culmen from the non-feathered base of the upper mandible to its distal end, 4) tail length, from the point of insertion of the two central rectrices to the end of the longest rectrix, 5) tarsus length, from the posterior junction of the tibiotarsus and the tarsometatrsus to the junction of the latter with the middle toe. We measured only non-molting birds in adult plumage. In a few cases we measured the left wing or leg if the right one was damaged. All measurements were made by KJS and were determined to be statistically repeatable by a repeated measures ANOVA of 52 randomly chosen specimens that were measured twice.

To examine temporal changes to geographic patterns of body size, we first estimated body size as the loading on the first principal component of a principal components analysis performed in Statistica Version 6 (StatSoft Inc. 2001) on the correlation matrix of log transformed measurements. Because *M. carolinus* males are larger than females we performed separate PCAs for each sex. We also used raw wing chord as a measure of body size because it is highly correlated with other measures of size and widely accepted as a proxy for bird size (Aldrich and James 1991, Ashton 2002). In the first analysis we divided our morphological data set into a pre-expansion period (1867–1949) and post-expansion period (1952–2009) based on the results of our mapping of the species' range (described above), which identified the decade of the 1950s as the onset of rapid range expansion. The pre-expansion sample comprises 281 specimens collected prior to 1950, and the post expansion sample comprises 124 specimens collected after 1954 and a single specimen from 1952. Previous studies have identified the year 1955 as the onset of rapidly warming temperatures in the eastern United States (McCoy 2012), thus our choice of 1950 is conservative with respect to the onset of the expansion period. We used linear regression to detect changes in the relationship between body size and latitude between the two time periods, interpreting slopes significantly greater than zero to be support for Bergmann's rule.

In a second analysis we analyzed the entire morphological data set using a mixed-effect linear model implemented in the lme4 package for the program R, version 2.3.0 (R Development Core Team 2006). In the model, body size (from PC 1) was the response variable, with sex as a random

effect, and latitude, year of specimen collection, and an interaction between latitude and year as covariates. We interpreted a significant contribution to the model of the ''year × latitude'' parameter to indicate that the relationship between body size and latitude was changing over the 105-year span of specimen data. Significance was tested in R with both a one-way ANOVA and by conducting a chi-squared likelihood ratio test that compared the full model with a model that did not include the year × latitude parameter.

We devised two methods for examining the evolution of body size at the expanding northern margin of the range of *M. carolinus*. In the first analysis, we used our plotted occurrence maps to identify the latitudinal range 41–44°N as the pre-expansion northern boundary. We then used a *t*-test to compare average body size of birds collected in that latitudinal range well before (1869–1939, $n = 33$ males and 32 females) and well after (1989–2009, $n = 13$ males and 15 females) the onset of the expansion period. We examined the residuals for these data to confirm the assumption of normality, and we eliminated the few specimens collected between 1940–1989 from this analysis so that there was a clear separation of the pre-expansion and post-expansion periods.

Our second analysis compared the body size of ''pioneers'' collected near the new northern front (north of 44.5°N, 1970–2009) to birds collected near the old northern front (41–44°N) to determine if larger birds predominate in the colonization of new areas. Unfortunately, there have been few museums actively salvaging and collecting specimens in the last few decades in the northeastern United States and southern Canada, and there are very few *M. carolinus* specimens from latitudes north of 44.5°N in collections. Therefore, this analysis was limited to males ($n = 14$) collected in the northwestern part of the species' range in Minnesota and Wisconsin.

RESULTS

Our graphical analysis of all three data sets reveals that the current range expansion began in the 1950s and has been characterized by expansion north and west, primarily following inland waterways and the Atlantic coast (Fig. 1). In the 19th century and early decades of the 20th century, an era prior to the advent of coordinated bird survey projects in which extralimital records were routinely documented by collecting specimens, our museum dataset documents the occasional occurrence of vagrant individuals well to the north and west of the core range. These records are primarily of males collected between April–September, including a male from September 1897 in North Dakota, a pair from April 1898 in Arizona, a male from Colorado in 1899, and a male from eastern Massachusetts in May 1915.

All three datasets clearly indicate rapid range expansion over the last several decades and also reveal a seasonal component to the expansion, such that winter records (CBC) occur farther north and west than summer records (BBS; Fig. 2). The average expansion from 1970s to 2000s is 0.8162 degrees north latitude/decade for CBC data versus 0.5186 degrees north latitude/decade for BBS data. The rate of western expansion over this same time interval is generally slower, but is still higher for winter birds (0.4963 degrees west longitude/decade) than summer birds (0.2652 degrees west longitude/decade). Areas that were newly occupied by winter birds become occupied by breeding birds in the following 1–2 decades, as for example in the Hudson River/Lake Champlain valley of New York, and later in the Red River valley of Minnesota and North Dakota and along the Atlantic coast of New England and Canada (Fig. 2).

Whereas we find little evidence from our maps of expansion in the first half of the 20th century, CBC data indicate steady expansion of the northern and western fronts as documented by the mean latitude and longitude of the northernmost and western-most records (Figs. 3, 4). This pattern could be a result of the greatly expanding number of CBC circles over this time period, but we consider this cause unlikely because the geographic coverage of count circles in these decades was always much greater than the known range of Red-bellied Woodpeckers.

We found a positive correlation between body size (PC 1) and degrees north latitude in our pre-expansion sample, consistent with Bergmann's rule (Fig. 5). Slopes of regression lines were significantly different from zero for both males ($r^2 = 0.1848$, $P = 1.134 \times 10^9$) and females ($r^2 = 0.2254$, $P = 4.018 \times 10^9$). This relationship breaks down in the post-expansion sample (Fig. 5) for both males ($r^2 = 0.0161$, $P = 0.371$) and females ($r^2 = 0.0256$, $P = 0.351$). In the mixed-effects linear model for the entire sample of specimens, sex accounted for 52.32% of the variance in body size. Latitude ($t = 2.126$, $P < 0.001$) and year of collection ($t = 1.532$,

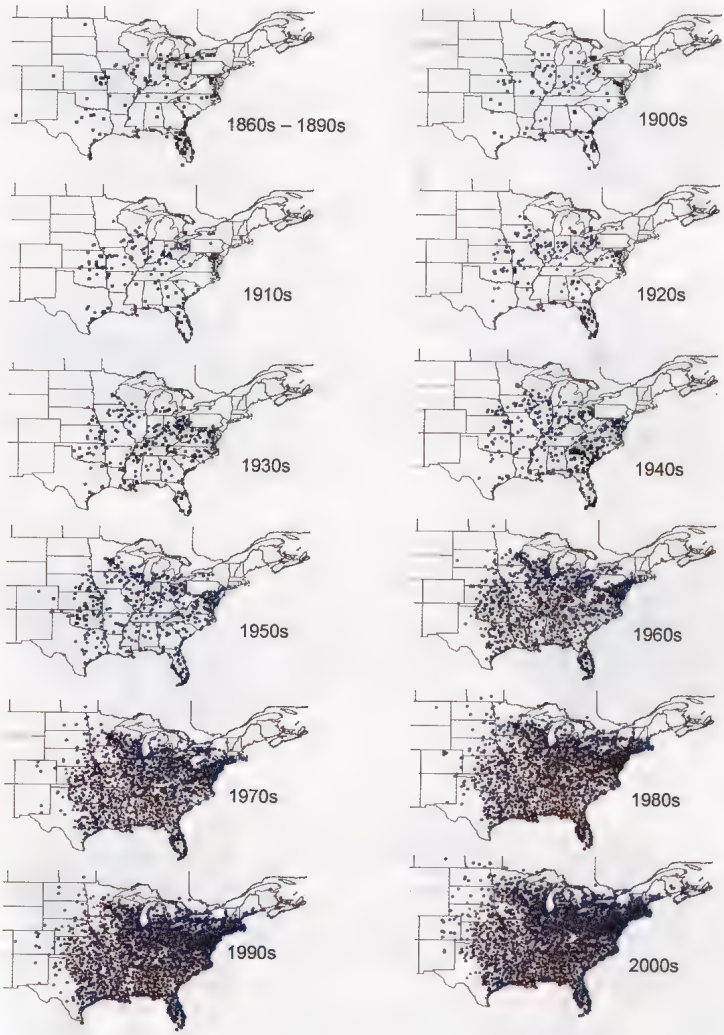


FIG. 1. Occurrence records by decade from museum specimens, Christmas Bird Counts (CBC), and Breeding Bird Surveys (BBS). Nineteenth century specimen records document wide ranging "pioneers" before a period of rapid range expansion to the north and west beginning in the 1950s. Expansion follows inland waterways and the Atlantic coast. The average rate of expansion from the 1970s to 2000s is slightly slower to the west (CBC 0.4963 degrees west longitude/decade; BBS 0.26517 degrees west longitude/decade) than to the north (CBC 0.8162 degrees north latitude/decade; BBS 0.5186 degrees north latitude/decade).

$P = 0.001$) had large effects on body size, and the interaction of latitude × year had a small but marginally significant effect on body size ($t = -1.970$, $P = 0.049$; $X^2 = 3.885$, $P = 0.048$), indicating a changing relationship between latitude and body size over the sampling period.

We also find evidence for breakdown of Bergmann's rule in our comparisons of body size

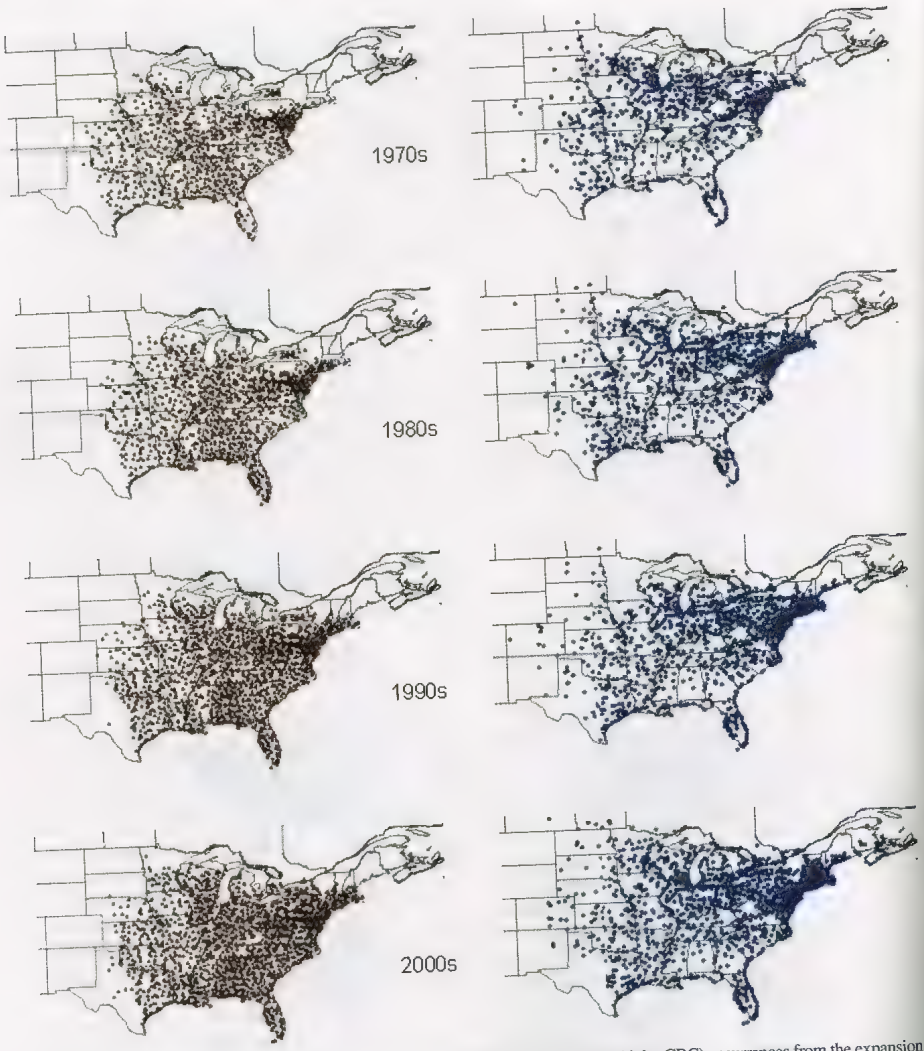


FIG. 2. Seasonality of range expansion. Plotting summer (left; BBS) and winter (right; CBC) occurrences from the expansion period shows that establishment of breeding in new areas lags behind colonization by non-breeders by about two decades.

of birds sampled before and after the onset of rapid range expansion at latitudes that correspond to the old northern periphery of the species' range. Birds collected near the old northern boundary (41–44°N in the period 1869–1939) were larger than birds collected from those same latitudes in recent decades (1989–2009) both in terms of wing chord (Females: mean wing chord = 127.87 mm pre-expansion and 125.71 mm post expansion; Males: mean wing chord = 131.52 mm pre-expansion and 130.08 mm post expansion) and PC 1 (Fig. 6). This difference was larger and significant in females ($P = 0.008$ for wing chord, $P = 0.004$ for PC 1), but not in males ($P = 0.083$ for wing chord, $P = 0.064$ for PC 1). Results of our second test indicate that ''pioneers'' (males

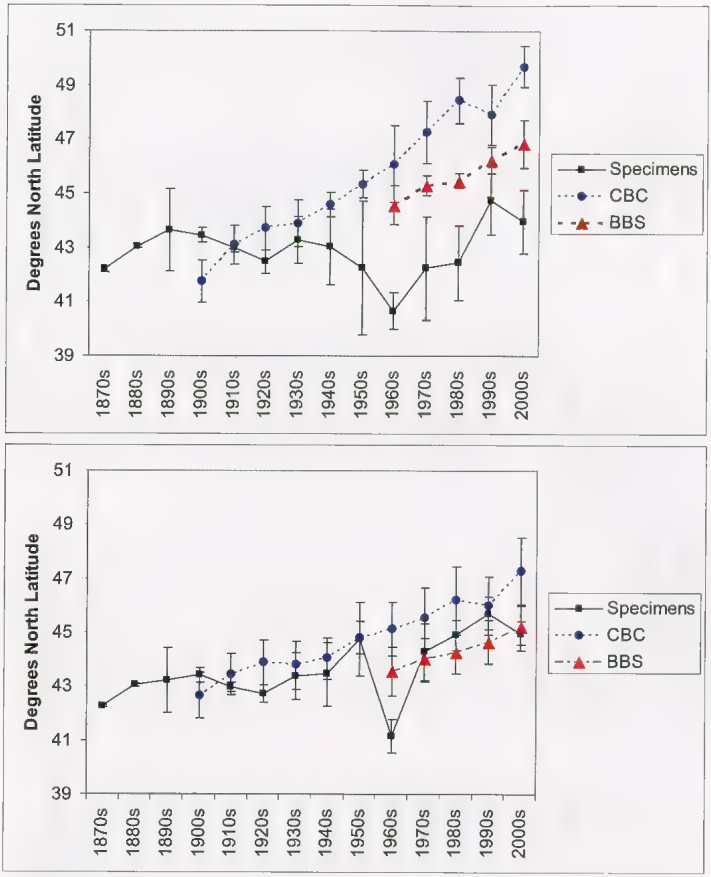


FIG. 3. Latitude of the northern edge of the range as determined by the (a) ten most northern occurrences and (b) the most northern 5% for each data set by decade has increased since 1950. Sample sizes for the most northern 5% graph (b) are as follows: Specimens n = 2–16, mean = 6.8; CBC n =52–1350, mean = 597.9; BBS n =625–1775, mean = 1209.4.

only) are not significantly larger than birds collected in the same time period near the old northern boundary (P = 0.69), and in fact are smaller than birds collected in the pre-expansion period near the old northern boundary (P = 0.019). This result is consistent with our finding that body size no longer correlates with latitude in the post-expansion sample of specimens.

DISCUSSION

Range Expansion.—Using three data sets, each with their own weaknesses and strengths allowed us to document the dynamics of the range of *M. carolinus* over the last 150 years. Museum specimens provide the longest history and document vagrants well, but the idiosyncratic and opportunistic nature of specimen collection, as well as the general waning of collecting effort beginning in the 1950s, has resulted in some decades with very few specimen records. Thus, mean latitudes of the northern-most 10 specimens or the northern-most 5% of specimens from a decade (Fig. 3) have large standard deviations, especially in the most recent decades. The large standard deviation of specimen latitudes in the 1890s results from the 1897 specimen from North

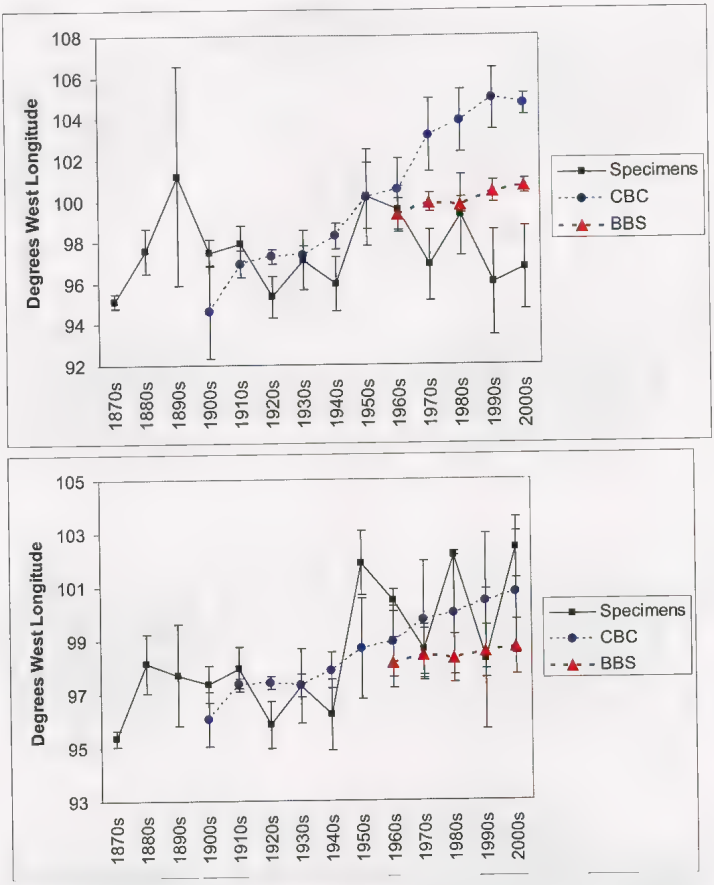


FIG. 4. Longitude of the western edge of the range as determined by the (a) ten most western occurrences and (b) the most western 5% for each data set by decade has increased since 1950. Sample sizes for the most western 5% graph (b) are as follows: Specimens n = 2–16, mean = 6.8; CBC n = 52–1,350, mean = 597.9; BBS n = 625–1,775, mean = 1209.4.

Dakota (UMMZ 53410), well to the north of the range at that time. Compared to coordinated survey projects like the CBC and BBS, museum collections do a poor job documenting the boundaries of ranges, but specimens uniquely document evolving phenotypes. In these times of rapid population dynamics and changing selective pressures, it is more important than ever that ornithologists judiciously collect specimens of even the most common bird species.

The CBC and BBS are more systematic surveys and document presence or absence throughout the range of Red-bellied Woodpeckers. CBC and BBS sampling effort has varied geographically over the years (Dunn et al. 2005), but even the first decades of these counts covered the known range of the Red-bellied Woodpecker, a vocal and conspicuous species that is not likely to be overlooked or confused with other species within its range. La Sorte and Thompson (2007) tracked latitudinal shifts in 254 species, including Red-bellied Woodpecker, by using CBC data to estimate the northern boundary (estimated as the latitude of the northernmost count circle reporting at least one individual), center of abundance (adjusted for survey effort by dividing the number

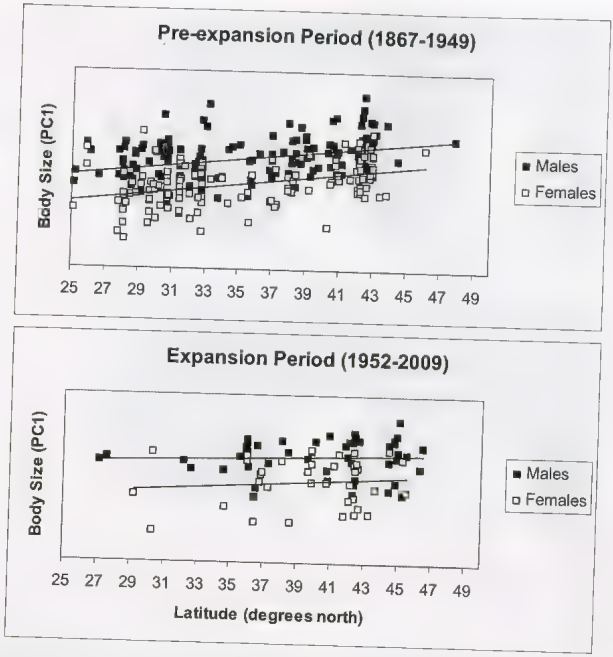

Pre-expansion Period (1867-1949)
Body Size (PC1)
25 27 29 31 33 35 37 39 41 43 45 47 49
Males
Females
Expansion Period (1952-2009)
Body Size (PC1)
25 27 29 31 33 35 37 39 41 43 45 47 49
Latitude (degrees north)
Males
Females

FIG. 5. Latitudinal variation in body size follows Bergmann's rule before 1950 (slope of regression line is greater than zero; males $r^2 = 0.1848$, $P < 0.0001$; females $r^2 = 0.2254$, $P < 0.0001$) but not after, during the expansion period from 1952–2000 (slope of regression line is not greater than zero, males $r^2 = 0.0161$, $P = 0.37$; females $r^2 = 0.0256$, $P = 0.35$).

of birds seen by party-hours), and center of occurrence of each species' winter range. For Red-bellied Woodpecker, they found northward movement in all three measures and that the rate of the latitudinal shift (measured as slopes from linear models) was faster at the northern boundary than the center of occurrence, but that the fastest movement was the center of abundance, hinting that a demographic population expansion over the last 40 years might be the driving force behind the expanding range of Red-bellied Woodpeckers, which we show has moved both north and west over the same time period.

Comparing data from winter (CBC) and summer (BBS) allowed us to identify a seasonal pattern of Red-bellied Woodpeckers' range expansion; new areas to the north and west are occupied first by winter birds and later by probable breeders. Counts conducted in the winter are likely to record the crop of new birds hatched the previous breeding season, some of which surely will not survive to breed. This pattern might be affected by the time-scale (decades) we chose for our analyses. Further study at shorter intervals or tracking of individual birds throughout the annual cycle might better resolve the lag time between colonization and the establishment of breeding sites.

The seasonal pattern we infer suggests a possible mechanism for Red-bellied Woodpeckers' range expansion. Whereas pairs defend territories during the breeding season, the territorial boundaries break down in the fall and the sexes occupy separate, largely non-overlapping foraging areas throughout the winter. Young of the year are driven away from the natal territory by the adults in late summer or early fall and can disperse large distances (Boone 1963). Both adults and juveniles have been observed to move into bottomland forest habitats in winter where mast is abundant (Kilham 1961). Since males are larger than females, those that disperse into areas with colder winters might be more likely to survive and establish territories the following spring. This hypothesis is consistent with our observations that vagrants collected far north or

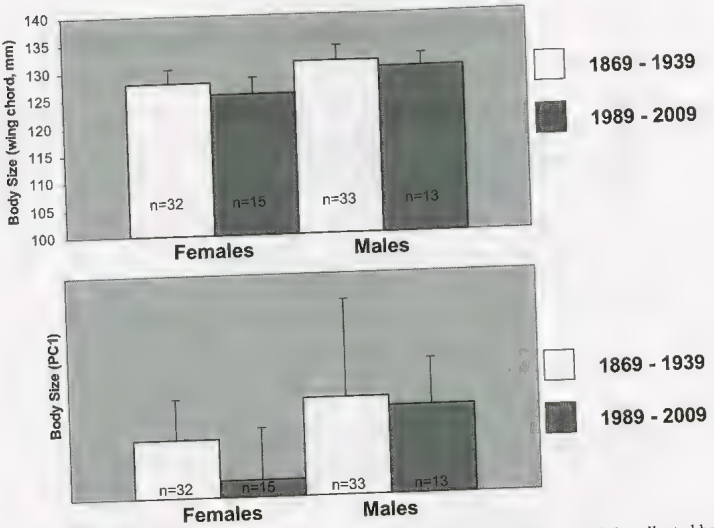


FIG. 6. Body size at the northern range boundary has changed as the front moves north. Birds collected between 41° N and 44°N were bigger in the pre-expansion era, both in overall body size (PC1) and wing chord. This difference is significant only for females (*t*-test results: females $P = 0.004$ for PC1, $P = 0.008$ for wing chord; males $P = 0.064$ for PC1, $P = 0.083$ for wing chord).

west of the core of the Red-bellied Woodpeckers' range tend to be non-breeding season males, and that expansion has proceeded west and north along river valleys. We predict that field surveys in late winter at the northern edge of the species' range would detect more males than females.

Bergmann's Rule.—We find evidence that prior to the onset of rapid range expansion, body size in Red-bellied Woodpeckers was positively correlated with latitude, a pattern of geographic variation known as Bergmann's rule. Both our regression analysis of pre- and post-expansion body sizes and our mixed-effects linear model of body size and latitude over a 105-year period indicate that the relationship between size and latitude in Red-bellied Woodpeckers has changed in recent decades. When ranges are stable and gene flow is low, populations may adapt to the prevailing local climate, resulting in a cline in body size such as we observed in Red-bellied Woodpeckers collected prior to 1950. To the extent that body size is a heritable genetic trait, latitudinal gene flow arising either from dispersal of individuals within a stable range or from range expansion will tend to disrupt the cline. We interpret the breakdown of Bergmann's rule to indicate that selection for large body size at the old northern boundary of the species' range has relaxed in recent decades, leading to an apparent shrinking in the average body size of birds at these latitudes. An alternative explanation is that northward expansion has been enabled by some factor other than climate, and that selection for increased body size is too weak to produce a detectable effect in our sample of birds from recent decades. Our small sample of pioneer specimens does a poor job of characterizing body size at the current northern boundary population, relative to our pre-expansion sample of specimens from the old northern front at 41–44°N. However, we do find that males from northern Wisconsin and Minnesota are significantly smaller than the specimens from the pre-expansion peripheral population there. For these reasons we interpret our results as support for the hypothesis of weakened selection for large body size at high latitudes, regardless of whether other factors, such as increased availability of bird feeders or decreased competition from other species, have facilitated the northward range expansion.

Bergmann's rule is thought to result from metabolic/morphological adaptation in response

to selection for cold-tolerance, and there is some indication that Bergmann's rule (in birds) is easier to detect in data drawn from winter distributions (Ramirez et al. 2008). The fact that the latitudinal gradient in mean body mass of bird species is stronger in winter is primarily due to seasonal migrations of smaller bodied birds toward the equator (Ramirez et al. 2008). This highlights the fact that endotherms follow several adaptive pathways to cold-tolerance including entrance to torpor, and behavioral pathways such as food storage, and use of warm microclimates (McNabb 2002). In addition to the metabolic advantage, larger body size may also provide greater starvation endurance, further complicating the factors that contribute to body size. We found a seasonal pattern with respect to range expansion but did not investigate seasonal variation in Red-bellied Woodpecker body size. An interesting extension of our work might be to greatly increase the number of specimens measured to enable comparisons of body size in winter birds versus summer birds.

The question remains as to whether the population-level morphological change we have documented is an evolved trait or a developmental response to changed conditions (i.e., phenotypic plasticity). Other studies have documented instances of population-level morphological change on decade time scales, including the studies showing reduced body size in response to climate warming that are consistent with Bergmann's rule (Yom-Tov et al. 2006, Van Buskirk et al. 2010, McCoy 2012), and a study that documented changes in wing shape over a period of 100 years in response to changes in forest fragmentation (Desrochers 2010). The key to establishing that changes such as these are evolved responses is documentation of heritability of these traits, either through pedigree analyses or experimental relocation studies.

ACKNOWLEDGMENTS

We thank the managers and compilers of the National Audubon Society's CBC and the USGS BBS data for providing data on Red-bellied Woodpecker sightings. We also wish to thank the curators and collections managers of the following natural history museums for specimen data or loans: American Museum of Natural History, Academy of Natural Sciences of Drexel University, Bell Museum of Natural History, Columbia Greene Community College, Carnegie Museum of Natural History, Canadian Museum of Nature, Cleveland Museum of Natural History, Cornell Museum of Vertebrates, Delaware Museum of Natural History, Denver Museum of Natural Science, Field Museum of Natural History, Illinois State University, University of Kansas Museum, Museum of Comparative Zoology, Michigan State University Museum, New York State Museum, Royal Ontario Museum, Sam Nobel Museum of Natural History, University of Michigan Museum of Zoology, University of Nebraska State Museum, U.S. National Museum of Natural History (Smithsonian), Yale Peabody Museum. We thank Laura Bried for assistance using ArcMap, Sara Scanga for advice regarding statistical analyses, and Alyssa FitzGerald and two anonymous reviewers for helpful suggestions that improved this manuscript.

LITERATURE CITED

ALDRICH, J. W. AND F. C. JAMES. 1991. Ecogeographic variation in the American Robin (*Turdus migratorius*). Auk 108:230–249.

AMERICAN ORNITHOLOGISTS' UNION (AOU). 1957. Checklist of North American birds. Fifth Edition. American Ornithologists' Union, Baltimore, Maryland, USA.

ASHTON, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography 11:505–523.

BEDDALL, B. G. 1963. Range expansion of the cardinal and other birds in the northeastern states. Wilson Bulletin 75:140–158.

BERGMANN, K. 1847. Ueber die Verhaltnisse der Warmeokonomie de Thiere zu Ihrer Grosse. Gottinger Studien 3:595–708.

BOONE, G. C. 1963. Ecology of the Red-bellied Woodpecker in Kansas. Thesis. University of Kansas, Lawrence, USA.

BURLEIGH, T. D. AND G. H. LOWERY, JR. 1944. Geographical variation in the Red-bellied Woodpecker in the southeastern United States. Occasional Papers of the Museum of Zoology, Louisiana State University. Number 17.

CHAPMAN A. D. AND J. WIECZOREK (Editors). 2006. Guide to Best Practices for Georeferencing. Global Biodiversity Information Facility, Copenhagen, Denmark.

DAVID, N., M. GOSSELIN, AND G. SEUTIN. 1990. Pattern of colonization by the Northern Mockingbird in Quebec. Journal of Field Ornithology 61:1–8.

DESROCHERES, A. 2010. Morphological response of songbirds to 100 years of landscape change in North America. Ecology 91:1577–1582.

DUNN, E. H., D. M. FRANCIS, P. J. BLANCHER, S. R. DRENNAN, M. A. HOWE, D. LEPAGE, C. S. ROBBINS, K. V. ROSENBERG, J. R. AAUER, AND K. G. SMITH. 2005. Enhancing the scientific value of the Christmas Bird Count. Auk 122:338–346.

ELLISON, W. F. 1993. Historical patterns of vagrancy by Blue-gray Gnatcatchers in New England. Journal of Field Ornithology 64:358–366.

EMLEN, J.T., M. J. DEJONG, M. J. JAEGER, T. C. MOERMOND, K. A. RUSTERHOLZ, AND R. P. WHITE. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradient. Auk 103:791–803.

GURALNICK R. P., J.WIECZOREK, R. BEAMAN, R. J. HIJMANS, THE BIOGEOMANCER WORKING GROUP. 2006. BioGeomancer: Automated Georeferencing to Map the World's Biodiversity Data. PLoS Biol 4(11): e381. doi:10.1371/journal.pbio.0040381.

HITCH, A.T. AND P. I. LEBERG. 2007. Breeding distribution of North American bird species moving north as a result of climate change. Conservation Biology 21:534–539.

HOLT, R. D. 2003. On the evolutionary ecology of species' ranges. Evolutionary Ecology Research 5:159–178.

INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE (IPCC). 2007. Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.

JACKSON, J. A. AND W. E. DAVIS, JR. 1998. Range expansion of the Red-bellied Woodpecker. Bird Observer 26:4–12.

JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:265–275.

KOELZ, W. N. 1954. Ornithological studies II. A new subspecies of Red-bellied Woodpecker from Texas. Contributions from the Institute for Regional Exploration 1:32.

KILHAM, L. 1961. Reproductive behavior of Red-bellied Woodpeckers. Wilson Bulletin 75: 227–234.

KRICHER, J. C. 1981. Range expansion of the Tufted Titmouse (*Parus bicolor*) in Massachusetts. American Birds 35:750–753.

LASORTE, F. A. AND F. L. THOMPSON. 2007. Poleward shifts in winter ranges of North American birds. Ecology 88:1803–1812.

MCCOY, D. E. 2012. Connecticut birds and climate change: Bergmann's Rule in the fourth dimension. Northeastern Naturalist 19:323–334.

MCGOWAN, K. J. AND B. ZUCKERBERG. 2008. Summary of results. Pages 15–42 *in* The second atlas of breeding birds in New York State (K. J. McGowand and K. Corwin, Editors). Cornell University Press, Ithaca, New York, USA.

MCNABB, B. K. 2002. The physiological ecology of vertebrates. Cornell University Press, Ithaca, New York, USA.

MEHLMAN, D. W. 1997. Change in avian abundance across the geographic range in response to environmental change. Ecological Applications 7:614–624.

MEIRI, S. AND T. DAYAN. 2003. On the validity of Bergmann's rule. Journal of Biogeography 30:331–351.

MEIRI, S., T. DAYAN, D. SIMBERLOFF, AND R. GRENYER. 2009. Life on the edge: carnivore body size variation is all over the place. Proceedings of the Royal Society 276:1469–1476.

PARMESAN C. AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

PYLE, P. 1997. Identification guide to North American birds. Part I. Slate Creek Press, Bolinas, California, USA.

R DEVELOPMENT CORE TEAM. 2006. R: a language and environment for statistical computing. R Foundations for Statistical Computing, Vienna, Austria.

RAMIREZ, L., J. A. F. DINIZ-FILHO, AND B. A. HAWKINS. 2008. Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. Global Ecology and Biogeography 17:100–110.

ROBINSON, L. J. 1977. The Red-bellied Woodpecker in Massachusetts—a case history of range expansion. Bird Observer of Eastern Masschusetts 5:195–200.

ROOT, T. L. 1988a. Energy constraints on avian distributions and abundances. Ecology 69:330–339.

ROOT, T. L. 1988b. Environmental factors associated with avian distributional boundaries. Journal of Biogeography 15:489–505.

ROOT, T. L., J. F. PRICE, K. R. HALL, S. H. SCHNEIDER, C. ROZENZWEIG, AND J. A. POUNDS. 2003. Fingerprint of global warming on wild animals and plants. Nature 421:57–60.

ROOT, T. L. AND J. D. WECKSTEIN. 1994. Changes in distribution patterns of selected wintering North American birds from 1901 to 1989. Studies in Avian Biology 15:191–201.

SHACKELFORD, C. E., R. E. BROWN, AND R. N. CONNER. 2000. Red-bellied Woodpecker (*Melanerpes carolinus*). The birds of North America. Number 500.

SHORT, L. L. 1982. Woodpeckers of the world. Delaware Museum of Natural History, Greenville, USA.

STATSOFT INC. 2001. Statistica. Version 6. Tulsa, Oklahoma, USA.

STILES, E. W. 1982. Expansion of the mockingbird and multiflora rose in the northeastern United States and Canada. American Birds 36:358–364.

TINGLEY M. W., W. B. MONAHAN, S. R. BEISSINGER, AND C. MORITZ. 2009. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences, USA 106:19637–19643.

VAN BUSKIRK, J., R. S. MULVIHILL, AND R. C. LEBERMAN. 2010. Declining body sizes in North American birds associated with climate change. Oikos 119:1047–1055.

WIECZOREK, J., Q. GUO, AND R. HIJMANS. 2004. The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. International Journal of Geographical Information Science. 18:745–767.

YOM-TOV, Y., S. YOM-TOV, J. WRIGHT, C. J. R. THORNE, AND R. DUFEU. 2006. Recent changes in body weight and wing length among some British passerine birds. Oikos 112:91–101.

ZINK, R. M. AND J. V. REMSEN, JR. 1986. Evolutionary processes and patterns of geographic variation in birds. Current Ornithology 4:1–69.

ZUCKERBURG, B. J., S. M. WOODS, AND W. F. PORTER. 2009. Poleward shifts in breeding bird distributions in New York State. Global Change Biology 15:1866–1883.

ZUCKERBERG, B., D. N. BONTER, W. M. HOCHACHKA, W. D. KOENIG, A. T. DEGAEATANO, AND J. L. DICKINSON. 2011. Climatic constraints on wintering bird distributions are modified by urbanization and weather. Journal of Animal Ecology 80:403–413.

The Wilson Journal of Ornithology 126(2):249–260, 2014

EXOGENOUS TESTOSTERONE IN MALE DOWNY WOODPECKERS LEADS TO REDUCED CALLING BEHAVIOR OF BOTH MALES AND THEIR FEMALE PARTNERS DURING THE NON-BREEDING PERIOD

JAMES S. KELLAM[1,3] AND JEFFREY R. LUCAS[2]

ABSTRACT.—Numerous studies have shown that testosterone (T) increases singing rates of passerine birds, but much less is known about the influence of T on non-song vocalizations, particularly in non-passerine species. Woodpeckers (order Piciformes) give several non-song vocalizations in a variety of social contexts throughout the year, including whinny and pik calls. We gave free-living male Downy Woodpeckers (*Picoides pubescens*) subcutaneous T implants during the non-breeding period to determine whether the incidences of these calls were greater among experimental males and their female partners compared to control males and females. We also tested whether calls were given more or less often when pair members were spatially proximate, and whether T treatment affected this pattern. Both call types were more likely given when pair members were nearby (<40 m), and this was true regardless of T treatment. Surprisingly, both males with T-implants and their female partners showed significantly lower incidences of whinny calls than control birds, and the female partners of T-implanted males also gave fewer pik calls. We attributed these patterns to the possible effect of T on non-vocal behaviors that influenced the social relationship between members of a pair. *Received 15 May 2013. Accepted 31 December 2013.*

Key words: bird calls, Downy Woodpecker, non-breeding season, pair bond maintenance, *Picoides pubescens*, testosterone.

Acoustic communication in birds can include a variety of signal types, many with multiple, overlapping functions. Birds use acoustic signals to attract mates, defend territories, warn against predators, and maintain social relationships such as the pair bond (Smith 1994, Nowicki and Searcy 2005). Because these activities are so important for reproductive success, there is an abundance of research on proximal mechanisms influencing the expression of acoustic signals. However, nearly all investigations of bird acoustic signals focus on songs, which are typically the most complex signals of a species' vocal repertoire and are most frequently given during the breeding season when reproductive hormones are at their highest concentrations. The effect of testosterone on birdsong is particularly strong: testosterone increases the propensity of males (and even females) to sing, the complexity of songs, and the duration of certain structural components of songs (Galeotti et al. 1997, Brenowitz et al. 1998, De Ridder et al. 2002, Van Roo 2004, Kurvers et al. 2008). These effects can be linked to testosterone-mediated increases in the size or activity of song control nuclei and the medial preoptic nucleus of the brain (Tramontin et al. 2000, Dawson et al. 2001, Ball et al. 2002, Brenowitz and Lent 2002). The relationship between testosterone and bird song is consistent with the widely supported hypothesis that elevated testosterone levels in birds and other animals facilitate male aggressive behaviors that relate to the defense of breeding territories and acquisition of mates (Wingfield et al. 1990).

Less is known about the effects of testosterone (hereafter T) on non-song forms of acoustic communication in birds, even though such signals may be expressed in a reproductive context (Marler 2004). Data suggest an activational role for T for some of these signals. For example, the advertisement calls of House Sparrows (*Passer domesticus*; Schwagmeyer et al. 2005) and Rufous Whistlers (*Pachycephala rufiventris*; McDonald et al. 2001), territorial calls of Red Grouse (*Lagopus lagopus scotica*; Mougeot et al. 2005), aerial alarm calls of domestic chickens (*Gallus gallus*; Gyger et al. 1988), and the sexually selected 'rusty gate' call of male and female Grey Partridges (*Perdix perdix*; Fusani et al. 1997) have all been shown to increase in frequency with supplemental T. The T-mediated call in the grouse was related to male territorial defense; in all other cases the non-song vocalizations were directed at females and could be used by females to assess male quality.

The role of T in facilitating behaviors during the non-breeding period has been investigated

[1] Department of Biology, Saint Vincent College, 300 Fraser Purchase Road, Latrobe, PA 15650, USA.
[2] Department of Biological Sciences, Purdue University, 915 W. State Street, West Lafayette, IN 47907, USA.
[3] Corresponding author; e-mail: james.kellam@stvincent.edu

much less than during springtime. However, pair bond relationships and courtship behaviors are present in some species at this time, and the expression of these behaviors has been found to positively correlate with T or T precursors (Sharp 1996, Wingfield et al. 1997, Frigerio et al. 2004). Testosterone concentrations in many temperate birds are near zero in fall and winter (i.e., "non-breeding baseline," Wingfield et al. 1990), but birds of some species become photostimulatory several months before breeding (Nicholls et al. 1988, Dawson 2008). This allows for small rises in testicular volume if not suppressed by environmental variables such as poor food supply, weather conditions, or lack of social stimulation (Dawson 2008). Plasma concentrations of T in birds between the non-breeding baseline and the breeding season levels that support male aggression are thought to facilitate sexual behavior including courtship (Wingfield et al. 1990).

The Downy Woodpecker (*Picoides pubescens*) is one species in which courtship behavior including copulation solicitations can be observed in winter (Kellam et al. 2004). Downy Woodpeckers are socially monogamous and year-round residents. They seem to defend small territories while nesting, but territorial defense away from a nest is poorly documented in the literature (Jackson and Ouellet 2002; but see Gordon and Confer 1996). Aggressive interactions appear to be more focused on mate selection than on spatial resources, since most (78%) same-sex aggressive displays observed from November through April took place within 40 m of a bird of the opposite sex (Kellam et al. 2004). Testosterone is found in males and females at low concentrations throughout the year (~5 ng/g feces or ~3 ng/ml plasma androgen equivalent), with population averages showing a small peak around 10 ng/g in April prior to egg laying (Kellam et al. 2004). Despite low population averages, some individuals during the nonbreeding period have levels of T equal to or exceeding those of breeding birds (Kellam et al. 2004).

A study using T implants in males from January through March was conducted to help determine the function of these elevated T levels. T-implanted males showed closer intrapair spatial association when experiencing a high degree of intrusions onto their home range by neighboring males (Kellam et al. 2006). T-males also showed reduced frequencies of male-male aggressive visual display and spatial association with same-sexed neighbors (Kellam et al. 2006).

The cause for a reduction in male-male interaction remains unclear. One possibility is that a T-male's dominance status or degree of readiness to respond to social challenge could have been maintained through other means and at a greater average distance from neighboring males, such as by increased vocalization rates (Boseret et al. 2006; also see De Kort et al. 2009). If T implants increased the calling rates of woodpeckers, this may have led to reduced interactions with other males.

Here, we used data collected during Kellam et al.'s (2006) study to examine the effect of T implants on the expression of two vocal signals given by free-living male Downy Woodpeckers and their female associates: 'whinny' calls and 'pik' calls. Whinny calls are loud and of relatively long duration (1.5 secs; Mahan 1996). They may be used in territorial defense, to assert dominance over neighbors, and to initiate contact with a mate (Kilham 1962, Short 1982, Ritchison 1999). There is little indication that males and females use the call in different contexts, but much of our understanding of this call comes from anecdotal reports and small observational studies. Mahan (1996) found that use of whinny calls by males varied across months, with most whinnies given in April. However, use of whinny calls by females did not vary across months (Mahan 1996). Pik calls are short notes averaging 5 msecs in duration (cf., 'teak' call of Mahan 1996) that may be given singly or repeated for several minutes at a time. Pik calls may serve as short-distance contact calls between mates, and may also indicate a state of mild alarm (Sullivan 1984, Ritchison 1999, Jackson and Ouellet 2002). Mahan (1996) found that pik calls were given year-round, but most frequently in April.

We predicted that whinny calls, because of their reported role in asserting dominance and territorial defense, would be given at greater rates by T-males than controls. No *a priori* prediction was made regarding the effect of T on the rate of pik calls, but the signal is included here because of its function in pair interactions, which could be altered by testosterone treatment. We also report on acoustic signals given by females because any change in male vocal behavior might affect the rate at which a female responds to the male signals. Lastly, we document whether whinny and pik calls are given more often when pair members are spatially proximate or more distant from one another, and whether T treatment alters this effect.

If testosterone has an effect on calls related to courtship or other pair interactions, the effect may be most evident when mates are close by.

METHODS

Our study was conducted at the Ross Biological Reserve, Tippecanoe County, Indiana from 5 January to 31 March 2001–2002. Details of the field methods were described in Kellam et al. (2006). In brief, 21 male and 24 female Downy Woodpeckers were captured over 2 years using manually operated tree-trunk mounted traps baited with suet. The population was studied previously (Kellam 2003a), so most individuals were marked with a unique combination of colored leg bands. For this study, woodpeckers were equipped with a 1.1-g radio transmitter (BD-2, Holohil Systems, Carp, ON, Canada; transmitter: body mass ratio ≤4%) using a leg-loop harness. The transmitters facilitated collection of behavioral data after each bird's release.

Testosterone Manipulation.—Male woodpeckers were transported a short distance from site of capture to a field laboratory where they were placed under anesthesia by intramuscular injection of saline containing a mixture of ketamine and xylazine (62.5 μg ketamine and 12.5 μg xylazine administered per gram of body mass). Ten males were randomly assigned to the experimental set (T-males) and given a subcutaneous Silastic tube implant (Dow Corning, Midland, Michigan; effective length: 7 mm, 1.47 mm i.d., 1.96 mm o.d.) packed with crystalline testosterone (T; Sigma-Aldrich, St. Louis, Missouri). The remaining 11 males (C-males) were given empty implants as a control. Radio transmitters were attached to all males before they were released at the site of capture after a 3-hr recovery period. Woodpeckers were recaptured after 5 weeks to remove spent radio transmitters and assess implant efficacy. T-males had significantly greater cloacal protuberance lengths and significantly higher concentrations of T in their feces than C-males (Kellam et al. 2006). The average T levels of T-males (15.2 ng/g feces; range 5.6–25.8 ng/g) were within the range shown by an unmanipulated population during April (range 1.9–39.4 ng/g; Kellam et al. 2004) and significantly higher than the average levels in C-males (5.5 ng/g; range 2.8–10.2 ng/g; Kellam et al. 2006).

Focal Observations.—We tracked each radio-marked woodpecker about once every 2 days for the ~30-day life of the transmitter. Data collection began 3 days following capture to minimize any residual effect of transmitter attachment and anesthesia (males only) on the woodpeckers' behavior. Focal observations were conducted during all daylight hours but ceased during periods of precipitation or high winds. The home ranges of experimental and control birds were intermingled throughout the study site as a result of random group assignments. Therefore, the mix of focal observations in the morning and afternoon always included each group.

Instantaneous scans were conducted every 10 mins during a 30-min focal observation that began as soon as a woodpecker was in view. These scans were used to document the identity and distance of conspecific associates, which were also wearing radio transmitters. Scans revealed that all woodpeckers tended to associate with a particular member of the opposite sex during focal observations, and these were considered to be mates. Such associations were observed in an earlier study of the same population as early as November (Kellam et al. 2004). The majority (67%) of these non-breeding partnerships persist into the breeding season, with much of the remainder (22%) breaking up because of death of a mate (Kellam et al. 2004).

We conducted time budget analyses during the same 30-min focal observations described above to measure the rate of acoustic signaling given by each woodpecker. Pik and whinny calls were recorded along with the behaviors of pecking, moving, looking and other activities as reported in Kellam et al. (2006). Birds rarely stayed in one place for more than a few secs at a time so we used a lapel microphone attached to an audiocassette recorder for hands-free recording of behavioral data. These audiocassettes were later transcribed in real time using event recorder software (a C++ program written by JRL) to count the number of calls given during each 30-min observation. Analyses were based on 7.2 ± 5.4 SD focal observations per bird. This represents a subset of a greater number of observations conducted on each bird for the purpose of delineating home range use (reported in Kellam et al. 2006) and male-female partnerships. Home range observations did not include time budget data, so they could not be used to quantify vocalization frequencies. Overall, the number of focal observations per bird varied because of differences in transmitter battery life and by some

TABLE 1. Number of 30-min focal observations conducted on Downy Woodpeckers used to analyze the effect of testosterone (T) implants on vocalization rates.

Group	*n*	Focal observations	Mean (and range of) observations/bird	Observations with whinny calls	Observations with pik calls
Control males	11	76	6.9 (1–16)	18	15
Control females	16	85	5.3 (2–12)	22	24
T-males	10	103	10.3 (7–18)	7	13
T-females	8	62	7.8 (4–19)	8	10

birds flying across a river. No direct hormone manipulations were conducted on females, but females were classified as T-females if they were the mate of a T-implanted male. Otherwise, females were classified as C-females. By chance, T-males and T-females had a greater average number of focal observations per bird than the control groups (Table 1). We included sampling rate as a variable in our statistical analyses to reduce any bias this may have caused (see below).

Social Context of Vocalizations.—It was beyond the design of our experiment to record the non-vocal behavioral responses of conspecifics receiving the vocal signals of the woodpecker under focal observation. However, if a non-focal individual gave a call during our observations, we were able to document it. Of particular interest was whether the calls of the woodpecker being observed were reciprocated by the mate. We noted the identity of the responding conspecific (when known), the latency of response, and the call type used (whinny or pik). Information on call reciprocation in this species has not been published elsewhere and it may clarify the function of whinny and pik calls with regards to pair bond maintenance. We assumed calls were reciprocated by the mate if the mate gave a vocal signal within 9 secs of a call made by the bird under focal observation. This 9-sec window was determined by looking at the distribution of latency values. There was a natural gap between 9 secs and 15 secs and another between 22 secs and 31 secs. To be conservative in our assumption of reciprocation, calls given by mates more than 9 secs after a call by the focal individual were assumed to be coincidental rather than responses to the initial call.

Statistical Analyses.—We hypothesized that T-treated males would utter whinny calls at a higher rate than control males, and that T treatment might also affect the rate of pik calls. Two repeated-measures statistical tests were carried out for males, one for each vocal signal. Two other models were run to analyze frequencies of female pik and whinny calls. We used SAS software (Version 9.3, SAS Institute, Cary, NC, USA) to construct generalized linear mixed models (PROC GLIMMIX; Littell et al. 2006) that tested whether the response variable, calls per hour, was dependent on T-treatment. Each bird was observed multiple times, so bird identity was used as a random, repeated factor. Goodness of fit for each model was confirmed following Littell et al. (2006) using the variable χ^2/df, which was near 1.00 in all cases. Significance was assumed at $\alpha = 0.05$.

There were some focal observations in which a woodpecker gave a series of repeated piks for several minutes, and pikking rates calculated for these observations were much higher than the 0–2/hr range typical of most observations. It is unclear whether a long series of piks has a different biological meaning than just a few piks scattered throughout a focal observation. If single piks and a series of piks are given in response to different stimuli, the pikking rate as calculated by piks per hr might be biased in a way that was independent of testosterone treatment since not all woodpeckers would be exposed to these different stimuli during our observations. Therefore, to minimize confounding effects, in a second analysis the rate of each vocalization was converted to a binomial distribution in which each focal observation was rated as to whether the vocalization was given or not given. We then constructed generalized linear mixed models that tested whether the binomial response variable (e.g., presence or absence of pik calls; hereafter 'binomial model') was affected by T treatment (T-implant or C-implant).

All models included a second independent variable and interaction term relating to whether the focal observation was being conducted on a woodpecker spatially proximate to its mate. Proximity to the mate was defined as a categorical variable indicating whether the woodpecker being

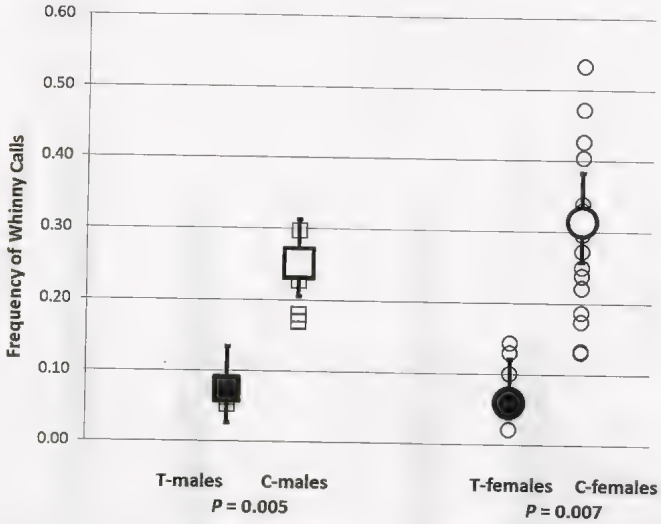


FIG. 1. Proportion of 30-min focal observations during which male and female Downy Woodpeckers gave at least one whinny call. Presented are least-squares means (± SE) output from repeated-measures mixed models run for each sex. Calling incidence of both males (large squares) and their female social partners (large circles) was significantly dependent on whether males had been given subcutaneous testosterone (T) implants or control (C) implants. Smaller squares and circles are the predicted values for individuals within each group as output from models that included implant type, proximity to the mate (>40 m or ≤40 m), sampling rate, and an interaction term.

observed was within 40 m of its mate during any one of the three scans conducted during a focal observation. A distance of 40 m was used because it ensured the two individuals were out of visual range. The function of whinny calls may be different depending on whether mates are in visual contact (i.e., pair interaction versus territorial functions). Since we did not specifically note whether male and female were in visual contact when giving whinny calls within 40 m of one another, we also ran the statistical models described above using shorter distances of association (10 m, 20 m, and 30 m). Results from these tests were not qualitatively different to the results reported below using the 40 m distance.

All models included a covariate representing sampling effort. Woodpeckers in each gender and experimental group were not observed an equal number of times (Table 1), so this variable helped account for any difference in vocalization rates or frequencies as a result of unequal sampling.

RESULTS

Whinny Calls.—One or more whinny calls were given by males in either treatment group during 14% (25 of 179) of focal observations. These calls were given during seven observations of four individual T-males and 18 observations of five individual C-males. Results from the repeated-measures binomial model showed that the propensity for T-males to give whinny calls was significantly lower than that of C-males ($F_{1,19}$ = 9.86, P = 0.005; Fig. 1). The effect of mate proximity on a male's likelihood to give whinny calls was not significant ($F_{1,12}$ = 0.69, P = 0.42; Fig. 2), nor was the interaction between hormone treatment and mate proximity ($F_{1,12}$ = 2.12, P = 0.17). Similarly, the average number of whinny calls per hour was significantly lower among T-males (1.1 ± 0.1 SE) compared to C-males (1.4 ± 0.1 SE; $F_{1,19}$ = 5.17, P = 0.035), and no significant effects of mate proximity were found ($F_{1,12}$ < 0.01, P = 0.95).

Overall, 20% (30 of 147) of focal observations conducted on females included one or more whinny calls; eight of the 30 calls were given by three individual T-females. The repeated-measures binomial model showed that T-females were significantly less likely to give a whinny call than C-females ($F_{1,22}$ = 8.85, P = 0.007; Fig. 1).

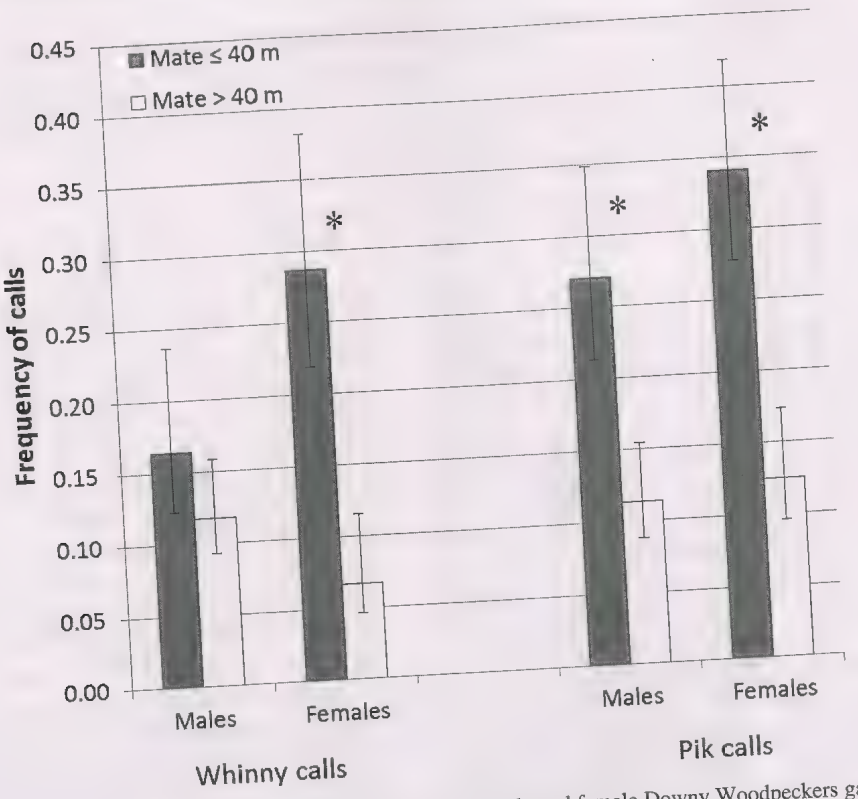


FIG. 2. Proportion of 30-min focal observations during which male and female Downy Woodpeckers gave at least one whinny or pik call. Presented are least-squares means (± SE) output from repeated-measures mixed models run for each sex and for each vocalization under the conditions of mate spatially proximate (≤40 m) or farther away. In the cases indicated by an asterisk, woodpeckers gave significantly fewer calls when the mates were separated by >40 m ($P < 0.05$).

Calling rate of T-females (1.1 ± 0.1 SE whinnies/hr) was significantly lower than C-females (1.5 ± 0.1 SE; $F_{1,22} = 12.94$, $P = 0.002$). Independent of T-treatment, females were significantly more likely to give whinnies when the mate was within 40 m ($F_{1,12} = 11.30$, $P = 0.005$; Fig. 1), and the number of whinnies per hr was greater ($F_{1,12} = 11.51$, $P = 0.006$). The interaction between T-treatment and distance from mate was not significant in either the binomial model ($F_{1,12} = 0.04$, $P = 0.85$) or the model testing whinnies per hr ($F_{1,12} = 1.89$, $P = 0.19$).

Pik Calls.—One or more pik calls were given by males in either treatment group during 16% (28 of 179) of focal observations. These calls were given during 13 observations of six individual T-males and 15 observations of six individual C-males. Results from the repeated-measures binomial model showed that there was no significant difference in the propensity to pik by T-males compared to C-males ($F_{1,19} = 1.49$, $P = 0.24$; Fig. 3). Likewise, male pik rate did not differ among T-males (1.5 ± 0.2 SE piks/hr) and C-males (1.4 ± 0.2 SE; $F_{1,19} = 0.09$, $P = 0.77$). The number of piks given per hour did not differ among males when the mate was nearby (≤40 m) versus far away ($F_{1,12} = 0.52$, $P = 0.49$). However in the binomial model, males were shown to be more likely to give pik calls when within 40 m of the mate ($F_{1,12} = 5.92$, $P = 0.030$; Fig. 2). There was no significant interaction between hormone treatment and mate proximity in either pik call model (binomial: $F_{1,12} = 0.27$, $P = 0.61$; rate: $F_{1,12} = 0.04$, $P = 0.85$).

Females gave pik calls during 23% (34 of 147) of focal observations. At least one pik call was given during observations of 14 females, including five T-females. Results from the repeated-measures binomial model showed that T-females were significantly less likely to call than C-females ($F_{1,22} = 4.40$, $P = 0.048$; Fig. 3). No difference was seen between T-females (1.8 ± 0.2 SE) and C-females (1.6 ± 0.2 SE) in the number of piks per hr ($F_{1,22} = 0.50$, $P = 0.49$). Female

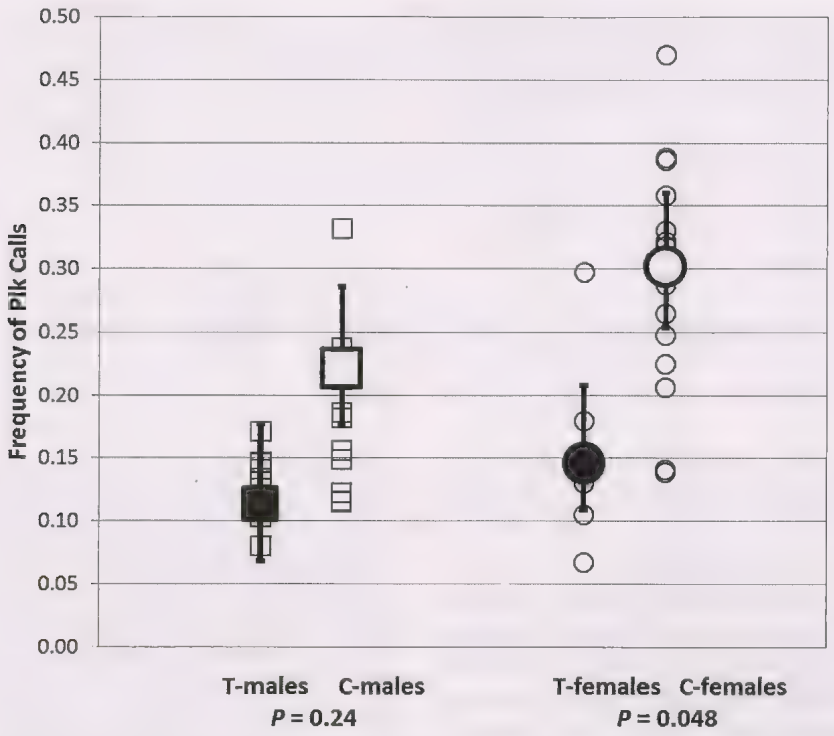


FIG. 3. Proportion of 30-min focal observations during which male and female Downy Woodpeckers gave at least one pik call. Presented are least-squares means (± SE) output from repeated-measures mixed models run for each sex. The incidence of calling in females was significantly dependent on whether their male social partner had been given a subcutaneous testosterone implant or control implant, but the males themselves showed no significant difference in calling related to their implant type. Smaller squares and circles are the predicted values for individuals within each group as output from models that included implant type, proximity to the mate (>40 m or ≤40 m), sampling rate, and an interaction term.

calling behavior was affected by mate proximity; females observed within 40 m of the mate were significantly more likely to give pik calls than females observed alone ($F_{1,12} = 9.37$, $P = 0.009$; Fig. 2), and they had a greater calling rate ($F_{1,12} = 10.08$, $P = 0.008$). There was no significant interaction found between T treatment and mate proximity using either model (binomial: $F_{1,12} = 1.63$, $P = 0.23$; rate: $F_{1,12} = 0.72$, $P = 0.41$).

Social Context.—Pik calls by both sexes and whinny calls by females were more likely to be given when a bird was spatially proximate to its mate, but sometimes the calls were given in other contexts (Table 2). There were 18 observations (of 117; 15%) when vocalizations were given but no conspecifics were detected within 40 m. Only 11of 35 (31%) observations on males associating within 40 m of another male documented a whinny call, and of those 11 observations, the mate was also present in five. Even at shorter inter-male distances, focal males only gave whinny calls half the time (9 of 18 observations when inter-male distance was ≤20 m, and 6 of 13 observations at <10 m).

Call reciprocation was fairly uncommon for both whinny and pik calls. There were 35 focal observations of males and females during which whinny calls were given. Six of these calls (17%) were reciprocated within 9 secs by the mate (average latency in response = 3.8 secs), and all were returned with a whinny call from the responding bird. In fact, extending the analysis to include six more observations beyond the 9-sec window, any call given by the mate up to 41 secs after a whinny call by the focal individual was always a whinny call rather than a pik call. Pik calls by focal individuals were reciprocated by the mate within 9 secs at a similar rate (6 of 44 focal observations; 14%). When pik calls were given by the focal woodpecker, there was an equal

TABLE 2. Number of focal observations of Downy Woodpeckers that included a vocalization when under different social contexts. Control and testosterone-treated woodpeckers are combined.

Social context[a]	Whinny calls		Pik calls	
	Male	Female	Male	Female
Association with mate[b]	11	24	18	27
Association with same-sex conspecific without mate	6	3	1	0
Other	4	1	2	2
No associations	4	2	7	5
Total	25	30	28	34

[a] Associations were defined as conspecifics observed within 40 m of one another on at least one occasion during a 30-min focal observation.
[b] With or without other conspecifics within 40 m.

likelihood that the mate would respond with a pik call or a whinny call (average latency = 6.2 secs).

DISCUSSION

Less than 22% of focal observations conducted on 35 individuals documented a vocalization, but this relatively low frequency was not unusual. Whinny call rates ranged from 1.1–1.5 per hour, which is greater than the 0.4 calls per hour documented by Mahan (1996) during non-breeding periods. Pik call rates ranged from 1.4–1.8, which is similar to the 1.5 calls per hour documented by Mahan (1996). Our results show that females gave both call types more frequently when located near the mate, and this was also true for males giving pik calls, independent of testosterone treatment. Males did not appear to give whinny calls any more frequently when near the mate than when away from the mate. However, the incidence of whinny calls given during close male-male interactions was not high, either, so it is unclear what circumstances most consistently lead to the production of whinny calls in males. What we do know is that the incidence and rate of whinny calls was reduced in the male and female experimental treatment groups. The incidence of pik calls was significantly lower in experimental females compared to controls, but no significant difference was found between male groups.

The role of testosterone is well known among vertebrate species in facilitating aggressive male-male interactions, especially when the interactions relate to defense of breeding territories or prospective reproductive partners (Wingfield et al. 1987). It thus seemed counterintuitive when Kellam et al. (2006) found that T-implanted male Downy Woodpeckers had significantly fewer close interactions with neighboring males than control males. Here we tested whether these same T-implanted males showed an increase in whinny vocalizations, which, like bird song (Catchpole and Slater 2008), could be used by neighboring males to assess a T-male's intentions or ability to defend the mate or territorial resources. Whinny calls have been described as signals used by males and females in territorial contexts, same-sex dominance interactions, and interactions with the mate (Kilham 1962, Short 1982, Ritchison 1999). Passerine song shares these same general functions (Nowicki and Searcy 2004), and supplementary T causes song rates to increase (Ball et al. 2002, Kurvers et al. 2008).

There were three possible outcomes of the experiment. First, our prediction could have been supported; T could have led to an increase in calling frequency. Second, T could have had no effect on calling frequency. Third, there could have been an unanticipated decrease in calling frequency related to the T treatment. This last outcome is best supported by our data. Failure to demonstrate the first outcome may be because of the time of year when our experiment took place and a reduced use of whinny calls to defend territory or advertise dominance status. Gordon and Confer (1996) reported that experimental playback of whinny calls and drums elicited whinny calls from resident Downy Woodpeckers. However, the woodpeckers ceased to respond to experimental playbacks after October (Gordon and Confer 1996). In winter, Downy Woodpeckers do not appear to defend exclusive territories since there is significant overlap in space use among individuals of the same sex (Matthysen et al. 1993, Kellam et al. 2006). Lack of territory defense could have prevented a T-mediated

increase in vocal behavior. Males of other temperate-zone species that are implanted with T and exposed to simulated territorial intrusions react more aggressively than control males exposed to the same stimulus (Wingfield and Soma 2002). The same simulated intrusions conducted in winter do not necessarily elicit the same aggressive responses by T-implanted males as in the breeding season (Wingfield and Soma 2002). Future studies on Downy Woodpeckers might still document a relationship between circulating T and whinny calls, but the effect may only be present when birds are defending territories. Likewise, T may influence one or more of the other acoustical signals given by breeding Downy Woodpeckers that have aggressive or sexual functions, including "kweek" calls, "tichrr" calls, and drumming and tapping behavior (see Ritchison 1999 for descriptions).

Even if T has no activational role in producing whinny calls during the winter season, a second question remains. Why did the T implants lead to a decrease in the rate and incidence of whinny calls? A review of the literature generally failed to find any studies where application of T caused or was correlated with a decrease in avian vocal behavior. One exception was Titus et al. (1997), who reported that yearling male Dark-eyed Juncos (*Junco hyemalis*) implanted with T during the pre-breeding plastic song phase showed lower song rates than controls, and fewer song types. The authors concluded that T given to the juncos prior to song crystallization may have disrupted normal singing behavior at the neurological level. The influence of T on non-song vocalizations has not been widely investigated (Marler 2004), and this is particularly true for non-passerine species that lack song control nuclei (Ball et al. 2002). In the absence of neurophysiological evidence that would explain T-mediated inhibition of vocal behavior, a more likely explanation for the decrease in whinny calls among T-males is that T treatment did not directly cause this pattern; rather, the negative relationship between T-treatment and calling rate was simply correlative.

For example, there could be a correlation between a male's vocal behavior and the frequency of his interactions with other males. If whinny calls are given during close male-male interactions, then a reduction in one behavior could correspond to a reduction in the other. Kellam et al. (2006) showed that T-male spatiotemporal associations with other males were 62% lower in frequency than controls, and T-males spent about 73% less time engaged in aggressive behaviors such as displacements, chases, and displays. In the present study, the incidence of whinny calls in T-males was reduced by 72% compared to control males (Fig. 1). However, analysis of social context found that whinny calls were not routinely given by males during same-sex encounters. Only 32–50% of such encounters involved a whinny call, depending on the minimum distance between interacting males. Therefore, the reduction in male whinny calls may not be wholly explained by the lowered number of male-male encounters experienced by T-males.

The incidences of female whinny calls and male and female pik calls were shown to be highest when mates were spatially proximate (Fig. 2). Calls given by one member of a pair were uncommonly reciprocated by the other pair member, but this is not necessarily inconsistent with the "contact calling" function proposed by previous authors (Jackson and Ouellet 2002). Kondo and Watanabe (2009) indicate that the receiver of a contact call may respond to the call in a non-vocal manner including moving toward or away from the signaler or by simply looking in its direction. The present study was not designed to monitor the kind of responses given by a conspecific receiving vocal signals.

Pik calls may be of particular importance in pair bond interactions because woodpeckers benefit from the pik calls of their partner. Sullivan (1984) showed that the efficiency of solitarily foraging Downy Woodpeckers (males and females combined) improved when she played a recording of pik calls and woodpecker foraging sounds. Sullivan concluded that woodpeckers rely on audible cues from conspecific flockmates to modify the frequency of anti-predator vigilant scans they interject between foraging bouts. Sullivan's (1985) later work showed that both male and female Downy Woodpeckers give preferential alarm calls ("tichrr" calls) when the mate is nearby. Combined, these results imply that mates can work together to protect one another from danger. There are numerous examples of this "mate investment" or "mate protection" behavior described in the avian literature (Hogstad 1995, Lemmon et al. 1997, Artiss et al. 1999, Kellam 2003b, Squires et al. 2007). This concept may help explain two results from our T-implant studies. We found T treatment in males led to a reduction in female pik calling (present study) as

well as reduced foraging efficiency in females (Kellam et al. 2006). If T-females found the male partner less attractive because of the T-implant, or if T-females perceived that their male partner was less invested in pair interactions (e.g., fewer whinny calls), the females could have reduced their own investment in the pair bond. This would have resulted in reduced female calling behavior and lowered female foraging efficiency as a result of increased vigilance requirements relative to controls.

Most songbirds show a predictable pattern in the level of reproductive hormones with peaks during the breeding season and minima typically measured in winter (Wingfield et al. 1990). This pattern changes in species with long-term pair bonding, such as Downy Woodpeckers. In particular, hormone concentrations can be relatively high in late winter/early spring and quite variable between individuals (Kellam et al. 2004). Testosterone levels can in turn affect association patterns between mates at these times (Kellam et al. 2006). Here we showed that testosterone levels also affect vocal signaling rates. Our results indicate that T-implants can lead to a reduction in calling behavior, a finding that contrasts with most other avian studies examining the effect of T on song and non-song vocalizations. The fact that the birds we used were free-living and in a non-breeding condition could explain the discrepancy. The concentration of T used in the implants was within the species' natural range but was still artificially high in experimental males compared to controls. It is unknown whether or not the same neurophysiological mechanisms responding to T in a breeding bird are operative during mid to late winter. In addition, relatively little is known about the biology of pair associations in birds before the breeding season. Our results suggest that this is an important time of year for the maintenance and regulation of long-term pair associations.

ACKNOWLEDGMENTS

We thank Z. Ligus, C. Mossman, and K. Munroe for comments on the manuscript, and K. Bondo, L. Braun, J. Hall, N. Haller, D. Kramb, R. Ritzel, D. Shelley, J. Vinyard, J. Wher, and B. Williams for assistance in the field. We are indebted to J. C. Wingfield for his support and guidance during execution of the project. We thank Ravines Golf Course, Tippecanoe County Parks, R. Kerber, R. Atwell, and C. Sahley for access to their property. The research was funded by Sigma Xi Grants-in-Aid of Research, the Indiana Academy of Science, and the Purdue Research Foundation. We thank Heath Manufacturing Co. for donating supplies.

All procedures relating to the observation, capture, handling, and hormonal manipulation of Downy Woodpeckers were approved by the Purdue University Animal Care and Use Committee under protocol 97-084-2.

LITERATURE CITED

Artiss, T., W. M. Hochachka, and K. Martin. 1999. Female foraging and male vigilance in White-tailed Ptarmigan (*Lagopus leucurus*): opportunism or behavioural coordination? Behavioural Ecology and Sociobiology 46:429–434.

Ball, G. F., L. V. Riters, and J. Balthazart. 2002. Neuroendocrinology of song behavior and avian plasticity: multiple sites of action of sex steroid hormones. Frontiers in Neuroendocrinology 23:137–178.

Boseret, G., C. Carere, G. F. Ball, and J. Balthazart. 2006. Social context affects testosterone-induced singing and the volume of song control nuclei in male Canaries (*Serinus canaria*). Journal of Neurobiology 66:1044–1060.

Brenowitz, E. A., L. F. Baptista, K. Lent, and J. C. Wingfield. 1998. Seasonal plasticity of the song control system in wild Nuttall's White-crowned Sparrows. Journal of Neurobiology 34:69–82.

Brenowitz, E. A. and K. Lent. 2002. Act locally and think globally: intracerebral testosterone implants induce seasonal-like growth of adult avian song control circuits. Proceedings of the National Academy of Sciences of the USA 99:12421–12426.

Catchpole, C. K and P. J. B. Slater. 2008. Bird song: biological themes and variations. Second Edition. Cambridge University Press, Cambridge, UK.

Dawson, A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Philosophical Transactions of the Royal Society of London, Series B 363:1621–1633.

Dawson, A., V. M. King, G. E. Bentley, and G. F. Ball. 2001. Photoperiodic control of seasonality in birds. Journal of Biological Rhythms 16:365–380.

de Kort, S. R., E. R. B. Eldermire, E. R. A. Cramer, and S. L. Vehrencamp. 2009. The deterrent effect of bird song in territory defense. Behavioral Ecology 20:200–206.

De Ridder, E., R. Pinxten, V. Mees, and M. Eens. 2002. Short- and long-term effects of male-like concentrations of testosterone on female European Starlings (*Sturnus vulgaris*). Auk 119:487–497.

Frigerio, D., K. Hirschenhauser, E. Möstl, J. Dittami, and K. Kotrschal. 2004. Experimentally elevated testosterone increases status signaling in male Greylag Geese (*Anser anser*). Acta Ethologica 7:9–18.

Fusani, L., L. Beani, C. Lupo, and F. Dessì-Fulgheri. 1997. Sexually selected vigilance behaviour of Grey Partridge is affected by plasma androgen levels. Animal Behaviour 54:1013–1018.

Galeotti, P., N. Saino, R. Sacchi, and A. P. Møller. 1997. Song correlates with social context, testosterone and body condition in male Barn Swallows. Animal Behaviour 53:687–700.

GORDON, A. L. AND J. L. CONFER. 1996. Do Downy Woodpeckers abandon their breeding territories in winter and relocate near a permanent food source? Kingbird 46:111–116.

GYGER, M., S. J. KARAKASHIAN, A. DUFTY, JR., AND P. MARLER. 1988. Alarm signals in birds: the role of testosterone. Hormones and Behavior 22:305–314.

HOGSTAD, O. 1995. Alarm calling by Willow Tits, *Parus montanus*, as mate investment. Animal Behaviour 49:221–225.

JACKSON, J. A., AND H. R. OUELLET. 2002. Downy Woodpecker (*Picoides pubescens*). The birds of North America. Number 613.

KELLAM, J. S. 2003a. Downy Woodpecker pair bond maintenance in winter: proximate and ultimate mechanisms. Dissertation. Purdue University, West Lafayette, Indiana, USA.

KELLAM, J. S. 2003b. Pair bond maintenance in Pileated Woodpeckers at roost sites during autumn. Wilson Bulletin 115:186–192.

KELLAM, J. S., J. R. LUCAS, AND J. C. WINGFIELD. 2006. The role of testosterone in male Downy Woodpeckers in winter home range use, mate interactions, and female foraging behaviour. Animal Behaviour 71:695–707.

KELLAM, J. S., J. C. WINGFIELD, AND J. R. LUCAS. 2004. Nonbreeding season pairing behavior and the annual cycle of testosterone in male and female Downy Woodpeckers, *Picoides pubescens*. Hormones and Behavior 46:703–714.

KILHAM, L. 1962. Reproductive behavior of Downy Woodpeckers. Condor 64:126–133.

KONDO, N. AND S. WATANABE. 2009. Contact calls: information and social function. Japanese Psychological Research 51:197–208.

KURVERS, R. H. J. M., M. L. ROBERTS, S. R. MCWILLIAMS, AND A. PETERS. 2008. Experimental manipulation of testosterone and condition during molt affects activity and vocalizations of male Blue Tits. Hormones and Behavior 54:263–269.

LEMMON, D., M. L. WITHIAM, AND C. P. L. BARKAN. 1997. Mate protection and winter pair-bonds in Black-capped Chickadees. Condor 99:424–433.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 2006. SAS system for mixed models. Second Edition. SAS Institute, Cary, North Carolina, USA.

MAHAN, T. A. 1996. Analysis of the acoustic signals of adult male and female Downy Woodpeckers. Thesis. Eastern Kentucky University, Richmond, USA.

MARLER, P. 2004. Bird calls: their potential for behavioral neurobiology. Annals of the New York Academy of Science 1016:31–44.

MATTHYSEN, E., D. CIMPRICH, AND T. C. GRUBB JR. 1993. Home ranges and social behaviour of the Downy Woodpecker *Picoides pubescens* in winter. Belgian Journal of Zoology 123:193–201.

MCDONALD, P. G., W. A. BUTTEMER, AND L. B. ASTHEIMER. 2001. The influence of testosterone on territorial defence and parental behavior in male free-living Rufous Whistlers, *Pachycephala rufiventris*. Hormones and Behavior 39:185–194.

MOUGEOT, F., A. DAWSON, S. M. REDPATH, AND F. LECKIE. 2005. Testosterone and autumn territorial behavior in male Red Grouse *Lagopus lagopus scoticus*. Hormones and Behavior 47:576–584.

NICHOLLS, T. J., A. R. GOLDSMITH, AND A. DAWSON. 1988. Photorefractoriness in birds and comparison with mammals. Physiological Reviews 68:133–176.

NOWICKI, S. AND W. A. SEARCY. 2004. Song function and the evolution of female preferences: why birds sing, why brains matter. Annals of the New York Academy of Science 1016:704–723.

NOWICKI, S. AND W. A. SEARCY. 2005. Song and mate choice in birds: how the development of behavior helps us understand function. Auk 122:1–14.

RITCHISON, G. 1999. Downy Woodpecker. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

SCHWAGMEYER, P. L., H. G. SCHWABL, AND D. W. MOCK. 2005. Dynamics of biparental care in House Sparrows: hormonal manipulations of paternal contributions. Animal Behaviour 69:481–488.

SHARP, P. J. 1996. Strategies in avian breeding cycles. Animal Reproduction Science 42:505–513.

SHORT, L. L. 1982. Woodpeckers of the world. Monograph Series 4. Delaware Museum of Natural History Greenville, Delaware, USA.

SMITH, W. J. 1994. Animal duets: forcing a mate to be attentive. Journal of Theoretical Biology 166:221–223.

SQUIRES, K. A., K. MARTIN, AND R. I. GOUDIE. 2007. Vigilance behavior in the Harlequin Duck (*Histrionicus histrionicus*) during the preincubation period in Labrador: Are males vigilant for self or social partner? Auk 124:241–252.

SULLIVAN, K. A. 1984. Information exploitation by Downy Woodpeckers in mixed-species flocks. Behaviour 91:294–311.

SULLIVAN, K. A. 1985. Allarm calling by Downy Woodpeckers in mixed-species flocks. Auk 102:184–187.

TITUS, R. C., E. D. KETTERSON, AND V. NOLAN, JR. 1997. High testosterone prior to song crystallization inhibits signing behavior in captive yearling Dark-eyed Juncos (*Junco hyemalis*). Hormones and Behavior 32:133–140.

TRAMONTIN, A. D., V. N. HARTMAN, AND E. A. BRENOWITZ. 2000. Breeding conditions induce rapid and sequential growth in adult avian song circuits: a model of seasonal plasticity in the brain. Journal of Neuroscience 20:854–861.

VAN ROO, B. L. 2004. Exogenous testosterone inhibits several forms of male parental behavior and stimulates song in a monogamous songbird: the Blue-headed Vireo (*Vireo solitarius*). Hormones and Behavior 46:678–683.

WINGFIELD, J. C., G. F. BALL, A. M. DUFTY JR., R. E. HEGNER, AND M. RAMENOFSKY. 1987. Testosterone and aggression in birds. American Scientist 75:602–608.

WINGFIELD, J. C., R. E. HEGNER, A. M. DUFTY JR., AND G. F. BALL. 1990. The "Challenge Hypothesis":

theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. American Naturalist 136:829–846.

WINGFIELD, J. C., J. JACOBS, AND N. HILLGARTH. 1997. Ecological constraints and the evolution of hormone-behavior interrelationships. Pages 22–41 *in* The integrative neurobiology of affiliation. Volume 807 (C. S. Carter, I. Lederhendler, and B. Kilpatrick, Editors). New York Academy of Sciences, New York, USA.

WINGFIELD, J. C. AND K. K. SOMA. 2002. Spring and autumn territoriality in Song Sparrows: same behavior, different mechanisms? Integrative and Comparative Biology 42:11–20.

The Wilson Journal of Ornithology 126(2):261–268, 2014

TESTOSTERONE PRODUCTION IN NON-BREEDING NORTHERN CARDINALS (*CARDINALIS CARDINALIS*): IS TEMPERATURE INFLUENTIAL?

JODIE M. JAWOR,[1,3] JEFFREY D. HOOKER,[1] AND RICHARD MOHN[2]

ABSTRACT.—In seasonally breeding birds annual changes occur in hormone production by the hypothalamic-pituitary-gonadal (HPG) axis as individuals transition between breeding and non-breeding condition. Typically, some external environmental cue induces the observed changes; changes in day length, corresponding to change of seasons, are a strong cue for HPG axis activity in many species. Some species use cues other than day length as their primary initiator of breeding, and a number of light-sensitive species incorporate other cues to initiate breeding. Northern Cardinals (*Cardinalis cardinalis*) exhibit individual variation in when breeding begins and circulating testosterone is present throughout the year. Chemical tests of HPG axis responsiveness indicate that many individuals have an activated HPG axis as early as December. Here we use GnRH injections to assess whether individuals with active HPG axes prior to the winter solstice and increasing day lengths, may be influenced to initiate breeding by low temperatures experienced at the time of GnRH challenge. We found that while a significant number of individuals had active HPG axes prior to the winter solstice, there was no effect of low temperatures. We suggest that broader environmental patterns and additional cues may be influential to breeding in cardinals as opposed to only immediate temperature changes. *Received 9 July 2013. Accepted 24 December 2013.*

Key words: *Cardinalis cardinalis*, GnRH challenge, Northern Cardinals, seasonality, testosterone.

In seasonally breeding species there are significant annual changes in behavior and physiology as individuals move between breeding and non-breeding condition (Dawson and Sharp 2007). During these transitions recrudescence and regression of the gonads occur, accompanied by changes in hormone production by the hypothalamus, anterior pituitary, and gonads (the hypothalamic-pituitary-gonadal [HPG] axis) (Gorbman and Sower 2003, Dawson and Sharp 2007, Leska and Dusza 2007, Wingfield et al. 2003, Tökölyi et al. 2012, Watts and Hahn 2012, Wingfield et al. 2012). Alteration in HPG axis activity and transition through breeding stages has been strongly linked to changes in day length in many species (Hahn et al. 2009).

Changes in day length indicate upcoming changes in seasons, temperatures, and resources. In the temperate zone, increasing early spring day lengths stimulate the elevated production and release of gonadotropin-releasing hormone (GnRH) from the hypothalamus (e.g., photostimulation; Cho et al. 1998, Leska and Dusza 2007, Stevenson et al. 2009, Saab et al. 2010, Stevenson et al. 2012). The production of GnRH from the hypothalamus increases anterior pituitary output, in particular luteinizing hormone (LH). Increased LH leads to increased steroid hormone and gamete production (gonadal recrudescence). As circulating steroid levels, particularly testosterone (T), increase a variety of T-dependent reproductive behaviors begin to be shown. For the majority of species in the temperate zone, during the mid- to late-summer, gonadal regression will begin; individuals become photorefractory, or no longer stimulated by long day lengths. With this, steroid hormone levels and gamete production drops, and the release of GnRH and LH decrease (Hahn and Ball 1995; Cho et al. 1998; Meddle et al. 2006a, b; Dawson 2005; Leska and Dusza 2007). Following a number of short winter days, photoregression is ended and individuals enter a photosensitive state wherein the HPG axis is ready to respond once day lengths again become longer (Deviche et al. 2000, Dawson and Sharp 2007, Stevenson et al. 2011). Species following this pattern of reproductive changes in response to day length typically have absolute refractoriness and are strict seasonal breeders (Hahn et al. 2009).

However, not all species use changes in day lengths as their primary cue for modification of HPG axis activity, and many photoperiodic species use non-photic cues as auxiliary information to fine tune exactly when they initiate reproduction (Hau 2001, Wingfield et al. 2003,

[1] University of Southern Mississippi, Department of Biological Sciences, 118 College Drive, #5018, Hattiesburg, MS 39406, USA.

[2] University of Southern Mississippi, Department of Educational Studies and Research, 118 College Drive #5093, Hattiesburg, MS 39406, USA.

[3] Corresponding author; e-mail: Jodie.Jawor@usm.edu

Caro et al. 2007, Dawson and Sharp 2007, Ball and Ketterson 2008, Tökölyi et al. 2012, Watts and Hahn 2012, Wingfield et al. 2012). In particular, species that rely on difficult to acquire or unpredictable resources for breeding, or in species where photoperiod is not extremely variable, there may be stronger reliance on cues other than changes in day length for the control of reproduction (Deviche and Sharp 2001; Deviche et al. 2006; MacDougall-Shackleton et al. 2006; Moore et al. 2006; Small et al. 2007, 2008; Tökölyi et al. 2012, but see Goymann et al. 2012 where a tropical species uses minor variations in day lengths). In these flexible, more opportunistic breeders, non-photic cues trigger changes in HPG axis activity and hormone production.

The Northern Cardinal (*Cardinalis cardinalis*) is a non-migratory, temperate-zone songbird (Halkin and Linville 1999) that displays a long breeding season (~7 months in the population under study here, mid-Mar to Oct) with strong individual variation in when reproduction is initiated (starts over a 1–2 month continuum). Cardinals are probably best described as a more flexible breeder with relaxed long-day requirements (see Hahn et al. 2009). Cardinals do display seasonality in reproduction, they experience annual cycles of gonadal recrudescence/regression (Jawor and MacDougall-Shackleton 2008; JMJ, pers. obs.), and show annual variation in some of the behaviors associated with breeding (e.g., song). Previous research has also found year-round circulating levels of T (Jawor 2007) in cardinals and non-breeding HPG axis activity (DeVries et al. 2011).

While investigating T production in non-breeding cardinals, DeVries et al. (2011) found that many individuals have active HPG axes in December. Activity was assessed via GnRH challenges; a classic technique where injections of GnRH are used to investigate whether individuals are reproductively capable (Wingfield et al. 1979, 1991; Schoech et al. 1996; Hirschenhauser et al. 2000; Moore et al. 2002; Goymann and Wingfield 2004). With GnRH challenges, if an individual can respond to the injection with a production of T this is indicative of an individual with an active HPG axis. Previous work with cardinals in December included assessment after the winter solstice, a time after which day lengths begin to increase (a potentially strong reproductive cue). Here we limit our analyses of response to GnRH challenges to days before the winter solstice, when day lengths are still *decreasing*. We compare T levels observed during challenges to low temperatures experienced before the day of GnRH challenge to determine if temperature could have an impact on HPG axis activity in this species.

We have chosen temperature as a potential cue, and specifically low temperatures, for the following reasons. First, in the southeastern United States temperature can be extremely variable in a short time frame (temperatures in Dec can fluctuate between 10 °C and 26 °C in a matter of one week) and in late winter temperatures can be quite warm. First nests for cardinals in this population are typically found beginning in mid-March and there is the potential for nest initiation to be advanced in particularly warm years (JMJ, pers. obs.). Individuals that try to initiate breeding early will also need to avoid producing eggs when temperatures are lethally low to eggs. Second, cardinals are generalists in terms of foraging and they do not feed their offspring a particular food type, nor do they use a specific type of plant for nesting. It is unlikely that reproduction in cardinals is tied to some limited or specialized food/nesting resource and may be more reliant on low temperatures that are not damaging to eggs. Potentially, the HPG axis may be more 'attentive' to low temperatures being experienced than to other cues.

METHODS

Field Methods.—All work was completed at the Lake Thoreau Environmental Education and Research Center, Hattiesburg, MS, USA (31° 20′ N, 89° 25′ W) owned and maintained by the University of Southern Mississippi, Hattiesburg, MS, USA. All birds were captured in mist nets or walk-in traps baited with food (commercial bird seed mix). Birds were captured from 0600–0900 Central Standard Time (CST) on days with no precipitation (snow or rain). Captures took place from 1 December until 21 December in the years 2008–2012. Upon capture, birds were transported to a centralized area for banding and GnRH challenges. Following GnRH challenge and blood collection, all individuals were banded and released.

GnRH Challenges.—Challenges were administered to all captured individuals. Injection protocol followed that described by DeVries et al. (2011). Briefly, following initial blood collection (for pre-challenge T) 100 µl of chicken-GnRH-I

solution (2.5 mg GnRH in 100 µl of phosphate buffered saline [PBS] solution) was injected into the pectoralis muscles. After 30 min, a second blood sample (for post-challenge T) was collected. Birds were held in cloth holding bags in between sampling times. Dosage of GnRH and timing were determined in 2008 (outlined in DeVries et al. 2011), and no control PBS injections were given as cardinals have been shown to not respond to PBS with increases in T (DeVries et al. 2011).

Hormone Assays.—To assess circulating levels of T an ELISA immunoassay (EIA) for T was used (Enzo Life Sciences, Ann Arbor, MI, United States). Using methods developed for cardinals in Jawor (2007), T was analyzed in duplicate on an ELISA plate coated with a T capture antibody. This kit has low cross-reactivity with androstendione (7.2%), corticosterone (<0.001%), dehydroepiandrosterone (0.72%), dihydrotestosterone (<0.001%), and estradiol (0.40%); antibody sensitivity for T estimated at 5.67 pg/ml of plasma (DeVries and Jawor 2012). Samples had a small amount of tritiated T added to them (to allow for determination of extraction efficiency), extracted three times with diethyl ether (extraction efficiency 84%), and reconstituted in kit-supplied buffer. Following visualization procedures, plates were analyzed on an ELISA plate reader and levels of T were calculated with a four-parameter logistic curve-fitting program (Microplate Manager, Bio-Rad Laboratories, Inc.). Estimated levels were corrected for initial plasma volume used and incomplete recoveries. Pre- and post-injection samples for a single individual were analyzed on the same plate. Standards of known T concentration were included on each plate to allow determination of inter- and intra-assay variation. Intra-assay variation was 19% and inter-assay variation was 12%. An assay-correction factor was applied to T values to allow for across assay analysis (as in Jawor et al. 2006, DeVries et al. 2011).

Corticosterone (CORT) is associated with stressful events (such as capture and handling) and has been suggested, in some species, to interfere with T levels circulating in the plasma. DeVries et al. (2011, 2012) and DeVries and Jawor (2013) found that during GnRH challenges, levels of CORT do increase in cardinals but there is no co-variation between CORT and T levels pre- or post-injection. Because of limited sample availability, we did not assess CORT in this study.

Temperature Data.—In analyses, we included low temperatures from the day, week, and month prior to the GnRH challenge. Temperature data were obtained from the National Oceanic and Atmospheric Association (NOAA). Temperature data were from the Hattiesburg-Laurel Regional Airport (31° 27′ N, 89° 19′ W), which is ~20 min away from the study site.

Statistics.—Statistical analyses were done using SPSS (IBM SPSS Statistics Version 20, IBM Corporation). Levels of T post-GnRH challenge were used as the dependent variable in a multiple regression where pre-GnRH challenge T, Julian calendar date, low temperatures proceeding GnRH challenge, sex, and year were independent variables. The year 2010 served as the comparison variable for year. Levels of T were natural log corrected prior to analyses. In the multiple regression analysis, there were four (4) individuals identified as potential outliers (1+ standard deviation beyond next closest value) because of either their strong increases in T ($n = 2$) or their strong decreases in T ($n = 2$). Analyses were completed with these individuals in the dataset and again with these individuals removed from the dataset. Outcomes were different and both are reported here.

RESULTS

In total, 51 individuals were sampled (21 males and 30 females) over the course of this study (4 in 2008, 12 in 2009, 18 in 2010, 7 in 2011, and 10 in 2012). No individual was assessed more than one time in this analysis. All individuals assessed had measurable T both before and after GnRH challenge. Pre-injection T levels in males ranged from 0.097–1.480 ng/ml, and in females levels ranged from 0.079–1.270 ng/ml.

Of the 51 individuals assessed 30 responded (59%) with at least a 0.2 ng/ml increase in T following GnRH challenge. Within males, 14 of 21 (67%) responded with T increases, within females 15 of 30 (50%) responded. When assessing the distribution of those individuals who did not respond (e.g., either there was no change in T levels, or, there was a decrease in T) non-responders were distributed across the entire 21 day period of December. Put another way, non-responders were not limited to just the early part of December.

There were four individuals (all females and from 4 different years) who could be considered outliers, and analyses were completed both with

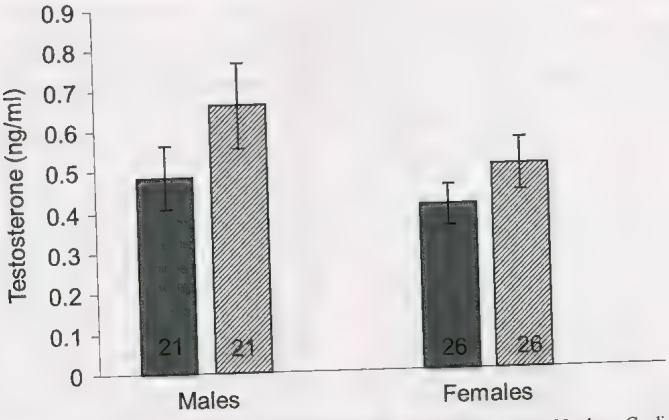


FIG. 1. Testosterone pre- and post-GnRH injection in male (left) and female (right) Northern Cardinals. Pre-GnRH injection levels are represented by solid bars, post-GnRH injection levels are represented by hatched bars. The four potential outliers have been removed, data are not separated by year.

and without these individuals. With the outliers retained in the analysis the model explained 20.4% of the variance ($R^2 = 0.337$, $F_{9,41} = 2.317$, $P = 0.033$) and there were no significant predictor variables, although pre-challenge T approached significance ($\beta = 0.461$, $P = 0.086$). With the potential outliers removed, the model explained 57.4% of the variance ($R^2 = 0.648$, $F_{9,37} = 7.580$, $P < 0.001$). Post-challenge T was significantly predicted by pre-challenge T ($\beta = 0.519$, $P = 0.012$), sex ($\beta = 0.135$, $P = 0.042$, males tend to have higher T, see Fig. 1), and the years 2008 and 2009 (2008; $\beta = 0.443$, $P = 0.058$: 2009; $\beta = 0.213$, $P = 0.023$, post-challenge T was higher in these years compared to other years in the study, see Fig. 2).

With regards to low temperatures prior to GnRH challenge, there were no effects on post-challenge

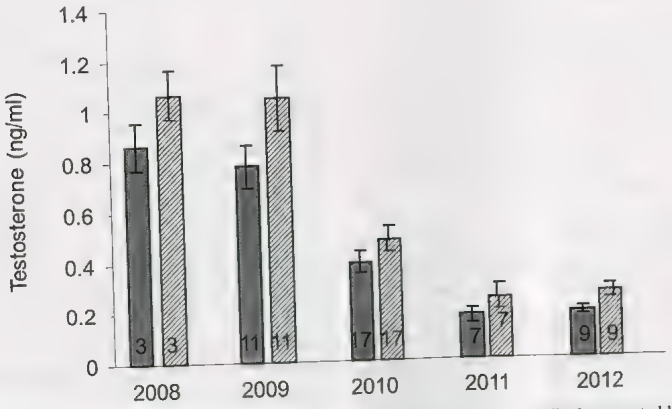


FIG. 2. Testosterone pre- and post-GnRH injection in male and female Northern Cardinals separated by year, but not separated by sex. Pre-GnRH injection levels are represented by solid bars, post-GnRH injection levels are represented by hatched bars. The four potential outliers have been removed.

T. Values for the model with outliers included were as follows: mean low in the month before challenge ($\beta = 0.026$, $P = 0.76$), mean low in the week before challenge ($\beta = 0.006$, $P = 0.72$), low the day before challenge ($\beta = -0.002$, $P = 0.85$). Values for the model with outliers removed were as follows: mean low in the month before challenge ($\beta = 0.039$, $P = 0.51$), mean low in the week before challenge ($\beta = 0.002$, $P = 0.89$), low the day before challenge ($\beta = 0.002$, $P = 0.75$).

DISCUSSION

Here we report on T production in response to GnRH challenge in non-breeding Northern Cardinals prior to the winter solstice, and increasing day lengths, and compare this to low temperatures experienced prior to challenges. Previous work with cardinals found that a number of individuals demonstrate active HPG axes in the month of December (DeVries et al. 2011). However, this work did not distinguish between pre- and post-solstice days. In the current work we specifically looked at HPG axis activity *prior* to the winter solstice, after which day lengths begin to increase and could start serving as a cue for changes in HPG axis activity. We did not find any indication that low temperatures were impactful to HPG axis activity. While Northern Cardinals could still be described as flexible breeders, because of their long breeding season and broad time scale for both initiation and cessation of breeding, they could not be described as opportunistic or relatively photoperiodic based on these findings.

We focused on low temperature as a potential cue as temperatures in the southeastern United States are variable and in some years quite warm. While there were no effects of low temperatures, there was a sex and year effect for analyses with potential outliers excluded. This suggests that overall, males have higher T or stronger responses than females and that in some years, responses or T levels can be higher than in others. There were broader year-to-year differences in temperature (annual highs and lows) as well as strong, annual variation in amounts of precipitation. The impact of year lends minor support to an influence of temperature or environment on HPG axis activity but potentially on a much broader time scale than assessed here.

Individuals responding to GnRH challenges in this study likely had exited the photorefractory state and had an HPG axis that was on the verge of natural, endogenous response. By injecting a large bolus of GnRH we triggered a reaction from an already primed axis, just circumventing the release of endogenous GnRH. This raises a question of why weren't all individuals in the population in a sensitive state at the time of assessment. It is unknown in cardinals just how many short days must pass before photorefraction ends or what other environmental factors may move cardinals into a sensitized state (see Saab et al. 2010). If this current research is identifying those individuals who had exited photorefraction, then it is clear that there is strong individual variation in when this process occurs. This variation could be a factor in how cardinals have adapted locally to the many different latitudes they are found in (Halkin and Linville 1999, Hahn and MacDougall-Shackleton 2008, MacDougall-Shackleton et al. 2009).

Throughout the month of December, T was circulating at a measurable level in both sexes. As with other studies with cardinals (Jawor 2007, DeVries et al. 2011), there is still the question of where exactly this T is coming from. In most avian species, T in the non-breeding season is undetectable and the gonads are considered inactive. It is possible that what is being observed here is one of two potential pathways for androgen production. In one scenario, it is possible that all the T observed in circulation is gonadal in origin; the gonads produce a continual amount of T even in their regressed state. Here, it is only after photoregression has ended that the gonads begin to produce variable levels of T in response to internal and external stimuli. Alternatively, in the non-breeding months the circulating T observed is largely adrenal in origin (modified from adrenal dehydroepiandrosterone), and it is again only after photoregression has been terminated that the gonads can begin responding to hypothalamic/pituitary stimuli with variable T production. Unfortunately, neither scenario can be supported exclusively at this point; further analyses are needed to determine differences between potential sources of T in the non-breeding season in this species, and the behavioral impacts this T has during the non-breeding season.

In more flexible breeders like the cardinal, there can be strong impacts of secondary cues for the initiation of breeding. While immediate temperatures were not impactful to HPG axis activity here, larger temperature patterns and additional environmental factors may be. In terms

of intra- and interspecific competition for breeding resources, species and individuals showing flexible breeding strategies/physiology may have an advantage over those that are not flexible. In years when favorable conditions occur early, they may be able to begin breeding sooner, continue breeding for a longer period of time, and perhaps produce more offspring overall. More work of this type, assessment of HPG axis activity, in other flexible breeders could provide interesting insights into whether HPG axis response to larger weather/temperature patterns is important to species showing this reproductive strategy. Additionally, how other aspects of reproductive ecology (e.g., the need for certain foods, the need for water) impact HPG axis activity and how multiple cues might together influence reproductive condition need to be assessed. Last, as environmental conditions are altered by human activity, all species will be impacted. A greater understanding of how environmental cues are responded to by the HPG axis will be needed as scientists and conservation biologists work to understand how species will respond to human-induced environmental change and survive that change.

ACKNOWLEDGMENTS

We would like to thank M. S. DeVries, B. M. Duckworth, K. Gentry, A. Holbrook, K. Trigg, A. Winter, and C. P. Winters for valuable assistance in the field and two anonymous reviewers for comments on an earlier version of this manuscript. Funding provided by The University of Southern Mississippi (USM). All work completed under USFWS banding permit 23479 and USFWS special purposes permit MB135338-0, Mississippi Department of Wildlife, Fisheries, and Parks permit 0319131, and USM's Institutional Animal Care and Use Committee (10081204).

LITERATURE CITED

Ball, G. F. and E. D. Ketterson. 2008. Sex differences in the response to environmental cues regulating seasonal reproduction in birds. Philosophical Transactions of the Royal Society B 363:231–246.

Caro, S. P., M. M. Lambrechts, J. Balthazart, and P. Perret. 2007. Non-photoperiodic factors and timing of breeding in Blue Tits: impact of environmental and social influences in semi-natural conditions. Behavioural Processes 75:1–7.

Cho, R. N., T. P. Hahn, S. MacDougall-Shackleton, and G. F. Ball. 1998. Seasonal variation in brain GnRH in free-living breeding and photorefractory House Finches (*Carpodacus mexicanus*). General and Comparative Endocrinology 109:244–250.

Dawson, A. 2005. Seasonal differences in the secretion of luteinizing hormone and prolactin in response to N-methyl-DL-aspartate in starlings (*Sturnus vulgaris*). Journal of Endocrinology 17:105–110.

Dawson, A. and P. J. Sharp. 2007. Photorefractoriness in birds – photoperiodic and non-photoperiodic control. General and Comparative Endocrinology 153:378–384.

Deviche, P., C. J. Saldanha, and R. Silver. 2000. Changes in brain gonadotropin-releasing hormone- and vasoactive intestinal polypeptide-like immunoreactivity accompanying reestablishment of photosensitivity in male Dark-eyed Juncos (*Junco hyemalis*). General and Comparative Endocrinology 117:8–19.

Deviche, P. and P. J. Sharp. 2001. Reproductive endocrinology of a free-living, opportunistically breeding passerine (White-winged Crossbill, *Loxia leucoptera*). General and Comparative Endocrinology 123:268–279.

Deviche, P., T. Small, P. Sharp, and K. Tsutsui. 2006. Control of luteinizing hormone and testosterone secretion in a flexibly breeding male passerine, the Rufous-winged Sparrow, *Aimophila carpalis*. General and Comparative Endocrinology 149:226–235.

DeVries, M. S., A. L. Holbrook, C. P. Winters, and J. M. Jawor. 2011. Non-breeding gonadal testosterone production of male and female Northern Cardinals (*Cardinalis cardinalis*) following GnRH challenge. General and Comparative Endocrinology 174:370–378.

DeVries, M. S. and J. M. Jawor. 2013. Natural variation in circulating testosterone does not predict provisioning rates in the Northern Cardinal, *Cardinalis cardinalis*. Animal Behaviour 85:957–965.

DeVries, M. S., C. P. Winters, and J. M. Jawor. 2012. Testosterone elevation and response to gonadotropin-releasing hormone challenge by male Northern Cardinals (*Cardinalis cardinalis*) following aggressive behavior. Hormones and Behavior 62:99–105.

Gorbman, A. and S. A. Sower. 2003. Evolution of the role of GnRH in animal (Metazoan) biology. General and Comparative Endocrinology 134:207–213.

Goymann, W. and J. C. Wingfield. 2004. Competing females and caring males. Sex steroid in African Black Coucals, *Centropus grillii*. Animal Behaviour 68:533–540.

Goymann, W., B. Helm, W. Jensen, I. Schwabl, and I. T. Moore. 2012. A tropical bird can use the equatorial change in sunrise and sunset times to synchronize its circannual clock. Proceedings of the Royal Society B 279:3527–3534.

Hahn, T. P. and G. F. Ball. 1995. Changes in brain GnRH associated with photorefractoiness in House Sparrows (*Passer domesticus*). General and Comparative Endocrinology 99:349–363.

Hahn, T. P. and S. A. MacDougall-Shackleton. 2008. Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response systems of birds. Philosophical Transactions of the Royal Society B 363:267–286.

HAHN, T. P., H. E. WATTS, J. M. CORNELIUS, K. R. BRAZEAL, AND S. A. MACDOUGALL-SHACKLETON. 2009. Evolution of environmental cue response mechanism: adaptive variation in photorefractoriness. General and Comparative Endocrinology 163:193–200.

HALKIN, S. L. AND S. U. LINVILLE. 1999. Northern Cardinal (*Cardinalis cardinalis*). The birds of North America. Number 440.

HAU, M. 2001. Timing of breeding in variable environments: tropical birds as model systems. Hormones and Behavior 40:281–290.

HIRSCHENHAUSER, K., E. MÖSTL, P. PÉCZELY, B. WALLNER, J. DITTAMI, AND K. KOTRSCHAL. 2000. Seasonal relationships between plasma and fecal testosterone in response to GnRH in domestic ganders. General and Comparative Endocrinology 118:262–272.

JAWOR, J. M. 2007. Testosterone in Northern Cardinals (*Cardinalis cardinalis*): possible influence of prolonged territorial behavior. Auk 124:331–338.

JAWOR, J. M. AND S. A. MACDOUGALL-SHACKLETON. 2008. Seasonal and sex-related variation in song control nuclei in a species with near-monomorphic song, the Northern Cardinal. Neuroscience Letters 443:169–173.

JAWOR, J. M., J. W. MCGLOTHLIN, J. M. CASTO, T. J. GREIVES, E. A. SNAJDR, G. E. BENTLEY, AND E. D. KETTERSON. 2006. Seasonal and individual variation in response to GnRH challenge in male Dark-eyed Juncos (*Junco hyemalis*). General and Comparative Endocrinology 149:182–189.

LESKA, A. AND L. DUSZA. 2007. Seasonal changes in the hypothalamo-pituitary-gonadal axis in birds. Reproductive Biology 7:99–126.

MACDOUGALL-SHACKLETON, S. A., M. KATTI, AND T. P. HAHN. 2006. Tests of absolute photorefractoriness in four species of cardueline finch that differ in reproductive schedule. Journal of Experimental Biology 209:3786–3794.

MACDOUGALL-SHACKLETON, S. A., T. J. STEVENSON, H. E. WATTS, M. E. PEREYRA, AND T. P. HAHN. 2009. The evolution of photoperiod response systems and seasonal GnRH plasticity in birds. Integrative and Comparative Biology 49:580–589.

MEDDLE, S. L., S. BUSH, P. J. SHARP, R. P. MILLAR, AND J. C. WINGFIELD. 2006a. Hypothalamic Pro-GnRH-GAP, GnRH-I and GnRH-II during the onset of photorefractoriness in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). Journal of Neuroendocrinology 18:217–226.

MEDDLE, S. L., J. C. WINGFIELD, R. P. MILLAR, AND P. J. DEVICHE. 2006b. Hypothalamic GnRH-I and its precursor during photorefractoriness onset in free-living male Dark-eyed Juncos (*Junco hyemalis*) of different year classes. General and Comparative Endocrinology 145:148–156.

MOORE, I. T., G. E. BENTLEY, C. WOTUS, AND J. C. WINGFIELD. 2006. Photoperiod-independent changes in immunoreactive brain gonadotropin-releasing hormone (GnRH) in a free-living, tropical bird. Brain Behavior and Evolution 68:37–44.

MOORE, I. T., N. PERFITO, H. WADA, T. S. SPERRY, AND J. C. WINGFIELD. 2002. Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. General and Comparative Endocrinology 129:13–19.

SAAB, S. S., H. S. LANGE, AND D. L. MANEY. 2010. Gonadotrophin-releasing hormone neurones in a photoperiodic songbird express Fos and Egr-1 protein after a single long day. Journal of Neuroendocrinology 22:196–207.

SCHOECH, S. J., R. L. MUMME, AND J. C. WINGFIELD. 1996. Delayed breeding in the cooperatively breeding Florida Scrub-Jay (*Aphelocoma coerulescens*): Inhibition or the absence of stimulation? Behavioral Ecology and Sociobiology 39:77–90.

SMALL, T. W., P. J. SHARP, AND P. DEVICHE. 2007. Environmental regulation of the reproductive system in a flexibly breeding Sonoran Desert bird, the Rufous-winged Sparrow, *Aimophila carpalis*. Hormones and Behavior 51:483–495.

SMALL, T. W., P. J. SHARP, G. E. BENTLEY, AND P. DEVICHE. 2008. Relative photorefractoriness, prolactin and reproductive regression in a flexibly breeding Sonoran Desert passerine, the Rufous-winged Sparrow, *Aimophila carpalis*. Journal of Biological Rhythms 23:69–80.

STEVENSON, T. J., D. J. BERNARD, AND G. F. BALL. 2009. Photoperiodic condition is associated with region-specific expression of GNRH1 mRNA in the preoptic area of the male starling (*Sturnus vulgaris*). Biology of Reproduction 81:674–680.

STEVENSON, T. J., T. P. HAHN, AND G. F. BALL. 2011. Variation in gonadotrohin-releasing hormone-1 gene expression in the preoptic area predicts transitions in seasonal reproductive state. Journal of Neuroendocrinology 24:267–274.

STEVENSON, T. J., T. P. HAHN, S. A. MACDOUGALL-SHACKLETON, AND G. F. BALL. 2012. Gonadotropin-releasing hormone plasticity: a comparative perspective. Frontiers in Neuroendocrinology 33:287–300.

TÖKÖLYI, J., J. M. MCNAMARA, A. I. HOUSTON, AND Z. BARTA. 2012. Timing of avian reproduction in unpredictable environments. Evolutionary Ecology 26:25–42.

WATTS, H. E. AND T. P. HAHN. 2012. Non-photoperiodic regulation of reproductive physiology in the flexibly breeding Pine Siskin (*Spinus pinus*). General and Comparative Endocrinology 178:259–264.

WINGFIELD, J. C., J. W. CRIM, P. W. MATTOCKS JR., AND D. S. FARNER. 1979. Responses of photosensitive and photorefractory male White-crowned Sparrows (*Zonotrichia leucophrys gamvelii*) to synthetic mammalian luteinizing hormone releasing hormone (Syn-LHRH). Biology of Reproduction 21:801–806.

WINGFIELD, J. C., T. P. HAHN, D. L. MANEY, S. J. SCHOECH, M. WADA, AND M. L. MORTON. 2003. Effects of temperature on photoperiodically induced reproductive development, circulating plasma luteinizing hormone and thyroid hormones, body mass, fat deposition and molt in Mountain White-crowned Sparrows, *Zonotrichia leucophrys oriantha*. General and Comparative Endocrinology 131:143–158.

WINGFIELD, J. C., R. E. HEGNER, AND D. M. LEWIS. 1991. Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding White-browed Sparrow-Weaver, *Plocepasser mahalis*. Journal of Zoology London 225:43–58.

WINGFIELD, J. C., K. SULLIVAN, J. JAXION-HARM, AND S. MEDDLE. 2012. The presence of water influences reproductive function in the Song Sparrow (*Melospiza melodia morphna*). General and Comparative Endocrinology 178:485–493.

The Wilson Journal of Ornithology 126(2):269–278, 2014

SINGING SEASIDE: PACIFIC WRENS (*TROGLODYTES PACIFICUS*) CHANGE THEIR SONGS IN THE PRESENCE OF NATURAL AND ANTHROPOGENIC NOISE

DANIELLE C. GOUGH,[1,4] DANIEL J. MENNILL,[2] AND ERICA NOL[3]

ABSTRACT.—Noise pollution poses a significant obstacle to vocal communication. Songbirds rely on acoustic signals for mate choice and territory defense, and masking of these signals can have negative fitness consequences. Prior investigations reveal that birds mitigate the negative effects of acoustic masking by increasing their signal amplitude or by singing with higher minimum frequencies. In this study, we evaluate the responses of male Pacific Wrens (*Troglodytes pacificus*) to natural ambient noise (ocean surf) and anthropogenic noise (highway traffic) in Pacific Rim National Park Reserve, B.C., Canada. Pacific Wrens, known for their complex songs, are specialists of old-growth forest. We hypothesized that Pacific Wrens would compensate for the effects of ambient noise in their environments through modifications to their songs that enhanced their transmission properties. Recognizing that longer, higher frequency, and more complex signals propagate better in noisy environments, we predicted that Pacific Wrens would increase the length of their songs, the length of the syllables within their songs, the number of syllables per song, and the minimum frequency of their songs. Recordings of 52 territorial Pacific Wrens showed that proximity to highway traffic noise had a significant effect on song duration but no significant effect on any of the other measured variables. Pacific Wrens that were recorded near the shoreline, however, sang songs with longer syllables, and higher intra-individual variation in song duration. Number of syllables, syllable minimum frequency, and song duration did not vary with distance from the shoreline. We conclude that natural and anthropogenic noise sources influence the singing behavior of Pacific Wrens. *Received 3 June 2013. Accepted 20 January 2014.*

Key words: acoustic masking, bird song, noise, Pacific Wren, signal transmission, *Troglodytes pacificus*.

Many animals use acoustic signals to communicate (Bradbury and Vehrencamp 2011). For songbirds, vocalizations play a central role in mate choice and territory defense (Catchpole and Slater 2008). The transmission properties of vocal signals are affected greatly by background noise (Lengagne et al. 1999, Brumm 2004, Brumm and Slabbekoorn 2005). Birds that emit acoustic signals face potential limitations by absorption of sound from the ground, the air, and forest vegetation along with masking from environmental noise, which occurs whenever the frequency of signals and noise overlap (Morton 1975, Wiley and Richards 1978, Lengagne et al. 1999, Brumm 2004).

Noise produced by abiotic sources such as ocean surf and wind, biotic sources such as the avian dawn chorus, or anthropogenic sources such as traffic, poses a barrier to efficient acoustic communication. Animals that live in the presence of noise may benefit by changing their vocalizations to compensate for the masking effects caused by noise. Many studies have shown that birds in urban areas sing at higher frequencies than those in non-urban habitats (Slabbekoorn and Peet 2003, Slabbekoorn and den Boer-Visser 2006, Nemeth and Brumm 2009, Hu and Cardoso 2010, Potvin et al. 2011); this may be an adaptive response, reducing spectral overlap with low-frequency noise. Common Nightingales (*Luscinia megarhynchos*) increase their signal amplitude in noisy conditions for improved signal transmission (Brumm and Todt 2002), and can adjust their vocal amplitude depending on the intensity of background noise (Brumm 2004). When Common Blackbirds (*Turdus merula*) encounter low-pitched traffic noise, they increase their song pitch because these songs can be produced at higher amplitudes (Nemeth et al. 2013).

The Acoustic Adaptation Hypothesis states that natural selection favors vocalizations fitted to a certain habitat for effective transmission between a signaler and a receiver (Morton 1975). There are costs to ensuring effective communication in a noisy environment, such as increased probability of detection by predators caused by increasing the duration and complexity of songs (Brumm 2004, Quinn et al. 2006). In addition, modifications to

[1]Environmental and Life Sciences Graduate Program, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.
[2]Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada.
[3]Biology Department, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.
[4]Corresponding author; e-mail: gdanielle20@gmail.com

songs in noisy conditions might improve signal transmission properties but simultaneously reduce attractiveness to females if the modified songs do not meet the preferred criteria of females (Halfwerk et al. 2011). Consequently, increases in anthropogenic noise that accompany expanding urbanization can pose severe challenges to a wide range of taxa, including birds (Reijnen and Foppen 1994, Rheindt 2003, Parris et al. 2009).

There are many studies that have focused on the responses of songbirds to traffic noise (e.g., Rheindt 2003, Slabbekoorn and Ripmeester 2008, Parris and Schneider 2009, Hanna et al. 2011). To our knowledge, no study has investigated the influence of ocean noise on the singing behavior of songbirds. However, one study has compared the structure of the songs of coastal breeding Eastern Willets (*Tringa semipalmata semipalmata*) with those of inland breeding Western Willets (*Tringa semipalmata inornata*; Douglas and Conner 1999); the masking and pulsing nature of ocean waves appeared to select for shorter, and higher frequency calls, delivered at an increased tempo, in the eastern sub-species. White-throated Dippers (*Cinclus cinclus*) vocalize at high frequencies to mitigate the acoustic masking in their noisy stream habitats (Brumm and Slabbekoorn 2005), and King Penguins (*Aptenodytes patagonicus*) increase their call output in windy environments (Lengagne et al. 1999). Thus, noise from ocean surf may play a significant role in shaping the vocal behavior of coastal birds. Studying the effects of natural noise on territorial songbirds is important for understanding the conditions under which birds can or will adapt their singing behavior or song structure.

In this study, our objective is to explore the behavior of songbirds in response to ambient noise from both natural sources of noise (ocean surf) and anthropogenic noise (traffic). We studied Pacific Wrens (*Troglodytes pacificus*), territorial songbirds well known for their complex song and large repertoire (Toews and Irwin 2008), that live in coastal forests of western Canada where they experience significant noise from both ocean surf and traffic sources. We hypothesized that Pacific Wrens would compensate for the effects of ambient noise in their environments by adapting their songs and singing behavior. Specifically, we predicted that wrens holding territories near the shoreline or a busy road would: (1) increase the duration of their songs and the syllables that comprise their songs. We base this prediction on the idea that longer songs and syllables are more detectable as they increase the opportunity to be heard above periodic noise sources (Lengagne et al. 1999), although we note that some studies have found shorter songs in noisy conditions (e.g., Douglas and Conner 1999, Slabbekoorn and Peet 2003, Slabbekoorn and den Boer-Visser 2006). We also predicted that: (2) wrens would increase the number of syllables in each song (increasing syllables improves the opportunity for information transmission; Lengagne et al. 1999, Brumm and Slater 2006); and (3) increase their minimum singing frequency (pitch) to counteract masking effects of low-pitched environmental noise (Slabbekoorn and Peet 2003, Wood and Yezerinac 2006). Finally, we predicted that there would be more intra-individual song variation for individuals singing in habitats near the highway or the ocean because song variability may be favorable in environments that experience varying levels of noise, and because highly variable sound environments may lead to intense sexual selection, which would favor complex songs (Medina and Francis 2012).

METHODS

Study Species and Site.—Pacific Wrens are small territorial songbirds that have only recently been separated from Winter Wrens (*Troglodytes hiemalis*), a species with a much wider circumboreal geographic distribution (Toews and Irwin 2008, Chesser et al. 2010). The geographic range of the Pacific Wren extends from west of the Rocky Mountains as far south as California and Utah and north to the southern coast of Alaska and the Aleutian Islands (Toews and Irwin 2012). Thus, the habitat of this species features both noise from increasing traffic in much of its range as well as noise from the Pacific Ocean.

We carried out this study in the Long Beach Unit of Pacific Rim National Park Reserve on the west coast of Vancouver Island in British Columbia, Canada. This unit is one of three geographically separated divisions of Pacific Rim National Park Reserve (hereafter 'the park') and is located between the communities of Tofino (49° 9.2′ N, 125° 54.1′ W) and Ucluelet (48° 55.5′ N, 125° 32′ W), British Columbia. The park is a protected area of land and sea within the Clayoquot Sound Biosphere Reserve. Our study area included a 16-km sandy beach adjacent to two types of forest: pristine ancient temperate rainforest and 40-year-old second-growth forests in areas that

were logged before the park was established in 1970. The forests are dominated by western redcedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*). The shrub layer is composed of salmonberry (*Rubus spectabilis*), red huckleberry (*Vaccinium parvifolium*), and salal (*Gaultheria shallon*).

Sources of Ambient Noise.—The Trans-Canada Highway (Highway 4) runs through the study site. The highway is a 2-lane road with a posted speed limit of 80 km/h. The traffic is largely made up by visitors to the park, locals, and delivery trucks to the two communities. Over one million people visit the site annually (Edwards 2005). Car traffic has increased steadily at the site, and is busiest in July and August (Edwards 2005). The number of cars entering the park per day has increased by 7%, 14%, and 8% for the months of May, June, and July, respectively from 2002–2011 (unpubl. road count data, Pacific Rim National Park Reserve, 2011). During the months of May, June, and July 2011, there was an average of 1,226, 1,541, and 2,000 vehicles (respectively) entering the park per day (unpubl. road count data, Pacific Rim National Park Reserve, 2011). Previous work has characterized the acoustic properties of traffic noise at other sites; it is known to be loud and low pitched (Slabbekoorn and Ripmeester 2008). Sound pressure level (SPL) measurements of morning traffic noise from two sites along the Trans-Canada Highway at our study site ranged between 80–90 dB (A-weighted decibels) SPL (collected 5 m away from the edge of the highway and averaged over a 10-min period in August 2012 using a Pyle PSPL25 sound level meter, Brooklyn, New York, USA; frequency range: 31.5 Hz to 8 kHz). Throughout, we refer to sound pressure level measurements as A-weighted decibel SPL (i.e., dBA).

A second major source of ambient noise is ocean surf. Our study site borders the Pacific Ocean, and crashing waves can be fairly strong, depending on wind direction and speed as well as water levels and tidal height. Like traffic noise, ocean noise is considered to be periodic noise, because noise levels decrease at low tide and between crashing waves. During August 2012, the average SPL measurement collected during the morning from four sites 5 m from the shore in Pacific Rim National Park Reserve was 73 dBA.

Experimental Design.—We recorded the songs produced by male Pacific Wrens at different distances away from the sources of ambient noise (ocean and traffic) within the Park during the breeding season from 0530–1300 Pacific Daylight Time (PDT) from 3 May to 12 July 2011. To minimize the influence of other noise sources, we only recorded individuals when there was little wind and no precipitation. We collected weather data (i.e., humidity, temperature, wind speed, and pressure) with a Kestrel weather tracker (4500 NV Pocket Weather Tracker). We used a handheld loudspeaker (Edge by Expedite; Hudson, WI, USA) to play back a conspecific Pacific Wren's song and stimulate the singing of individuals. All individuals received the same playback at the same volume level, which approximated the amplitude of a live singing Pacific Wren based on our assessment in the field. The playback was used for as long as necessary to stimulate singing of an individual (from 1 song to 10 min of playback at a rate of 5 songs/min).

We used a directional microphone (model: Audio-Technica AT8015; Stow, OH, USA) and a digital recorder (model: Marantz PMD670; recording settings: WAVE format, 44.1 kHz sampling rate, 16-bit accuracy) to record a total of 93 individuals for ≥30 min. The birds in this study were not individually marked. Instead, we distinguished between birds based on the location of their territories. We presumed that the birds we recorded were different individuals based on their geographic separation (i.e., individuals ≤200 m apart were not recorded). We entered each individual's location at the time of recording into a global positioning system (GPS; model: Garmin GPS 76CSX). We used the GPS coordinates of each recording location to determine the distance from each male to the nearest shore and to the nearest highway.

Estimation of Traffic and Ocean Noise as a Function of Distance.—We recorded the average noise level measurement during a 1-min period using the sound level meter at each of six positions moving away from noise sources (5 m, 25 m, 50 m, 75 m, 100 m, and 200 m) along 2–3 transects leading from each source. Both ocean surf and highway traffic are periodic noises; by calculating averages over a 1-min period, we generated a typical profile for what a nearby animal faces in terms of the amplitude of background noise. Distances from the shoreline or roadside were recorded using a hand-held GPS unit. Noise measurements were made in August 2012; we make the assumption that the noise

measurements from August are similar to noise measurements at the same sites in May through July when our bird recordings took place.

Analysis of Songs.—We used Avisoft SASLab Pro (version 5.1.20; R. Specht, Berlin, Germany) to generate spectrograms of songs from each of the recorded Pacific Wrens. From our 93 recordings, only 63 were of sufficiently high quality for detailed analysis. For each of the 63 males, we selected the first five songs that were not overlapped by the sounds of heterospecific animals and we used the 'automated parameter measurement' feature in Avisoft to extract detailed bioacoustic measurements (threshold setting: -15 dB relative to maximum; hold time: 5 ms). The use of automated parameter measurements minimized any subjectivity in collecting bioacoustic measurements. In all cases, we visually assessed the spectrograms to ensure that the automated parameter measurements were reasonable. We measured the song duration (ms), length of each syllable (ms), number of syllables (per song), and the syllable minimum frequency (Hz).

Data Analysis.—The response variables in this study were song duration, syllable length, number of syllables, and syllable minimum frequency. The independent variable was distance to noise source, whether to shoreline or edge of the highway. We verified that all response variables met the assumption of normality by inspecting histograms. Given that time of day can influence song characteristics (e.g., Dabelsteen and Mathevon 2002), and given that we recorded songs over an 8-hr period, we first tested for the effect of time of day on each response variable. When these regressions were not significant (for response variables syllable length, song duration, syllable minimum frequency), we proceeded with linear regressions of the song characteristics on distance to the noise sources. For one response variable, average number of syllables, we found a significant increase with time of day (regression equation: number of syllables = 118.6230 + 4.6630 decimal hour, $r^2 = 0.08$, $P = 0.023$); for this response variable we tested the effect of distance from source and time of day using multiple linear regression.

The path of the highway and the edge of the shoreline wind through our study site. At most locations, it was not possible for us to hear both the ocean surf and the traffic noise simultaneously. For wrens found within earshot range of both ocean and highway noise, we excluded birds that were within 100 m from one source, while testing the impacts of the second source (e.g., birds recorded within 100 m of ocean were excluded from regressions examining the impact of road noise). Five of the 63 birds recorded were excluded while testing the impacts of the ocean noise and 11 birds were excluded while testing the impacts of the highway noise.

To examine the effects of distance to the ocean or highway on the amount of variation within five songs of each individual, we performed a mixed model ANOVA for each of the response variables with distance to ocean and distance to the highway (near or far) as a fixed variable and the individual bird identity as a random factor. Near was considered to be 100 m or less from the source of noise and far was over a 100 m. These values were based on personal observation; after 100 m, our ability to detect the noise had decreased significantly. A variance-ratio test was performed subsequently given that the two sampled populations were normally distributed (Zar 2009).

We considered results to be statistically significant at $P < 0.05$. We plotted linear regressions for the song characteristics that varied significantly to determine whether the change in song characteristics matched the pattern of change in noise amplitude as a function of distance. Linear regressions were carried out in R version 2.13.1 (R Development Core Team 2011). Mixed model ANOVAs and verification of assumptions were performed using Statistica Version 7.0 for Windows (StatSoft, Inc. 2004).

RESULTS

Our recordings and noise level measurements demonstrated that both highway traffic noise and noise from ocean surf contribute substantial sources of noise (Fig. 1). Average traffic noise was measured at 85 dBA beside the highway, and dropped to 51 dBA 100 m away from the highway edge, while average ocean surf noise was measured at 73 dBA at the shore and 54 dBA 100 m from the ocean (Fig. 2). Songs of Pacific Wrens are long with a large number of syllables per song (Table 1). Minimum frequency varied minimally, whereas number of syllables and song duration varied moderately among individuals (Table 1).

Influence of Ocean Noise.—We found a significant negative relationship between average syllable

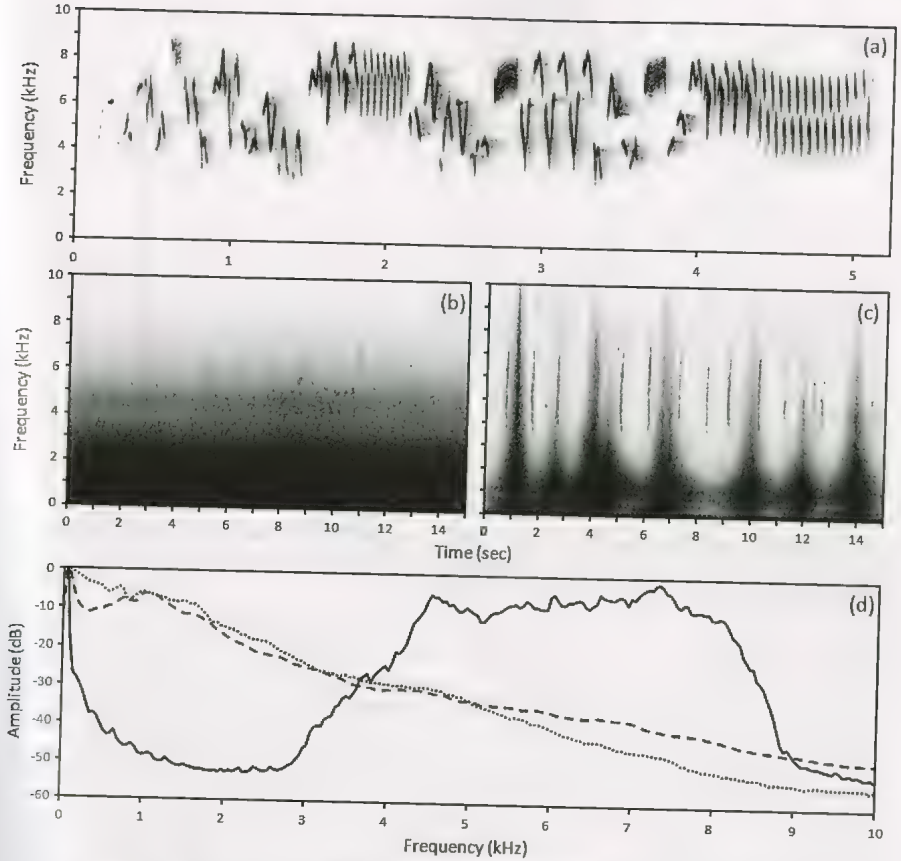


FIG. 1. Sound spectrograms of a typical song from a Pacific Wren (*Troglodytes pacificus*) (a), 15 secs of ocean noise (b), and 15 secs of highway noise (c) recorded in Pacific Rim National Park Reserve, British Columbia, Canada. Power spectra (d) are shown for a typical Pacific Wren's song (solid line), ocean noise (dotted line), and traffic noise (dashed line).

length and distance from the ocean ($r^2 = 0.09$, $n = 58$, $P = 0.02$; Fig. 3a; Table 2), a weak, non-significant effect on average number of syllables, and no effect of ocean noise on average syllable minimum frequency or song duration (Table 2). Song duration was significantly more variable within individuals near the ocean than individuals farther away (Variance-Ratio Test: $F_{10,51} = 2.68$, $P = 0.01$). The distance from the ocean showed no relationship with intra-individual variation for any other song characteristics.

Influence of Traffic Noise.—We found a significant positive relationship between average song duration and distance from the highway ($r^2 = 0.08$, $n = 52$, $P = 0.05$; Fig. 3b; Table 2). Distance to the highway did not have a significant effect on the average number of syllables, the average syllable minimum frequency, or the average syllable length of Pacific Wrens. We found no significant intra-individual variation for any of the response variables in relation to distance to the highway.

DISCUSSION

By studying variation in the songs of Pacific Wrens in relation to the singing birds' proximity to noise sources of roadsides and shorelines, we found that wrens sing significantly longer syllables and

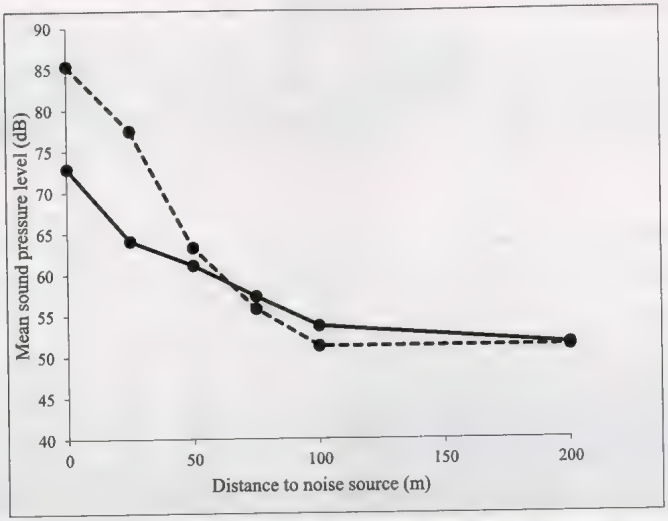


FIG. 2. Mean sound pressure levels (dBA) corresponding to varying distances from the ocean (solid line) and the highway (dotted line). Values at each distance are means from transects retreating from each source of noise ($n = 2$, except for 0 m and 25 m from ocean where $n = 4$ and 3, respectively).

with significantly more variable song durations near the ocean. Wren songs also varied with proximity to roadside: wrens sing significantly shorter songs near the highway. Therefore, our investigation reveals that the songs of Pacific Wrens show an influence of a natural noise source, the sound of the ocean surf, and an effect of an anthropogenic noise source, the sound of traffic, although the latter effect was opposite to the direction that we predicted.

Influence of Ocean Noise on Wren Song.—Average syllable length was higher for songs of individuals that were recorded near the ocean. This finding supports our prediction and previous studies that have found that prolonged signals increase the ability of a receiver to detect a signal (Lengagne et al. 1999). We found no significant relationship between song duration and distance to the ocean. Pacific Wrens that were recorded near the ocean did not have songs that contained more syllables than those birds singing in quieter environments. Although increasing syllables are hypothesized to increase redundancy of a signal and improve the amount of information being transmitted in a noisy environment, we found only a non-significant pattern of higher syllables near the shoreline, even though ocean noise was often loud enough to disrupt normal human conversation. In other species (e.g., King Penguins) the number of syllables per call increased as wind speed increased, starting at a wind speed of 8 m/s (Lengagne et al. 1999). Similarly, Chaffinches in noisier habitats increased serial redundancy to effectively transmit their message (Brumm and Slater 2006). The faster tempo of Eastern versus Western Willets provides another consistent

TABLE 1. Song characteristics of Pacific Wrens recorded at Pacific Rim National Park Reserve, British Columbia, Canada ($n = 63$).

Song characteristic	Mean ± SE	CV (%)
Syllable Length (ms)	16.01 ± 0.25	13
Song Duration (ms)	6222.91 ± 185.61	24
Syllable Minimum Frequency (Hz)	5387.81 ± 19.65	3
Number of Syllables (per song)	159.92 ± 4.56	23

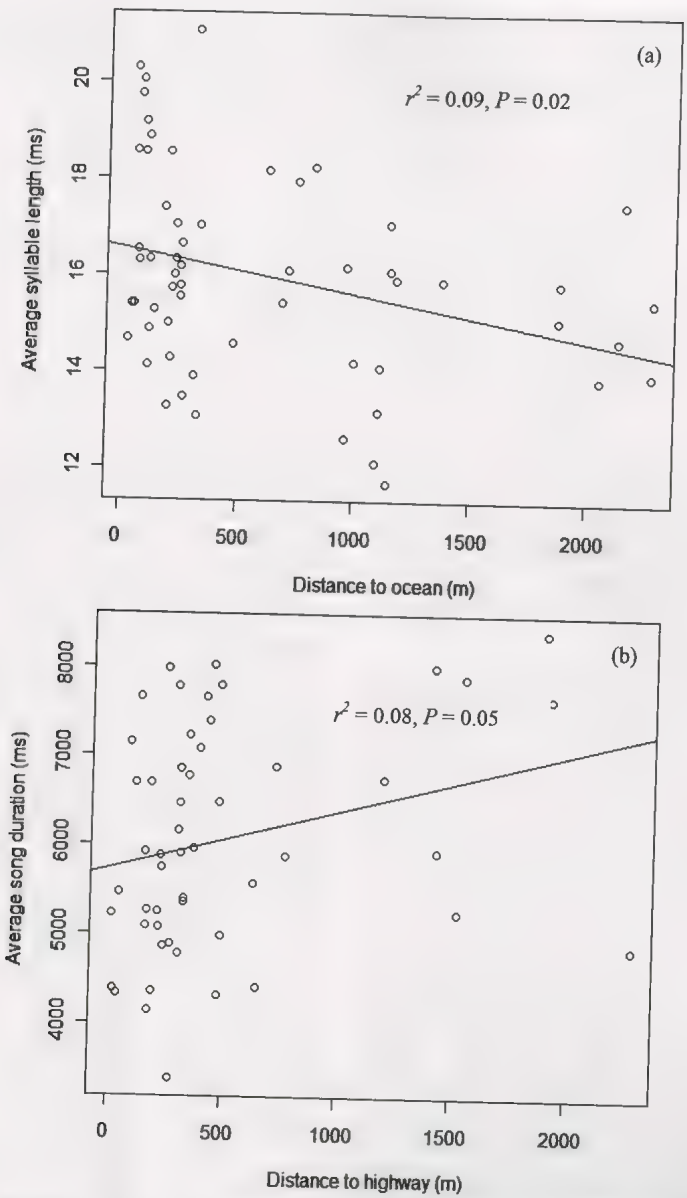


FIG. 3. Linear regression plots showing (a) a significant negative relationship between the average syllable length of Pacific Wrens' songs and distance from the ocean (regression equation: Syllable length = 16.5846–0.0009 distance to ocean) and (b) a significant positive relationship between the average song duration of Pacific Wrens' songs and distance from the highway (Song duration = 5735.5671 + 0.6478 distance to highway).

TABLE 2. Results of linear or multiple regression models for associations between distance to noise source (m; ocean surf or highway noise) and syllable length (ms), song duration (ms), syllable minimum frequency (Hz), and number of syllables (per song) of Pacific Wrens' songs along with corresponding F values of full models, P values, and r^2 values. Degrees of freedom for regressions with ocean and highway are 1,56 and 1,50, respectively.

Noise source	Regression equations	F	P	r^2
Ocean	Syllable length = 16.5846–0.0009 Distance to ocean	5.72	0.020	0.09
	Song duration = 6561.5072–0.4092 Distance to ocean	1.98	0.17	0.03
	Syllable minimum frequency = 5370.0000 + 0.0315 Distance to ocean	0.97	0.33	0.02
	Number of syllables = 134.3344–0.0123 Distance to ocean + 3.8652 Decimal hour	2.92	0.093	0.05
Highway	Syllable length = 15.6400 + 0.00002 Distance to highway	0.001	0.98	<0.01
	Song duration = 5735.5671 + 0.6478 Distance to highway	4.09	0.049	0.08
	Syllable minimum frequency = 5413.4264–0.0340 Distance to highway	0.89	0.35	0.02
	Number of syllables = 110.3000 + 0.0087 Distance to highway + 4.6780 Decimal hour	1.16	0.29	0.02

response to natural noise, with higher redundancy (Douglas and Conner 1999). The number of syllables in the songs of singing Pacific Wrens was moderately variable among individuals (CV = 23% of mean; Table 1), so this may have contributed to why we were unable to detect an effect of either noise source on this song characteristic.

We found no significant relationship between distance to ocean and syllable minimum frequency. Low-frequency signals experience greater acoustic interference from low-frequency noise than do high-frequency signals (Rheindt 2003, Parris and Schneider 2009). Given that Pacific Wrens' songs have relatively high frequency characteristics overall (Fig. 1), it is possible that the low-frequency noise from the ocean and the highway does not mask their songs, which would provide an explanation for the lack of observed effect in syllable minimum frequency.

We had predicted that there would be greater intra-individual variation in all song characteristics for wrens recorded near sources of noise but found that there was only greater intra-individual variation in song duration for individuals near the ocean (within 100 m) compared to far away from the ocean (>100 m). Although this was not tested, the within-individual variation in song duration may be because of interruptions in singing caused by crashing waves and hence analogous to the hypothesized function of shorter songs in Eastern Willets that can then be transmitted between the crashing of waves (Douglas and Conner 1999). In the case of Pacific Wrens, songs are generally much longer (up to 10 secs; Toews and Irwin 2012) than those of Willets and many other species, so varying song length during the waves would also ensure transmission of at least part of the song. The highly variable song length of birds singing at the ocean may help to explain why we did not find a significant change in song length as a function of distance to the ocean.

Influence of Traffic Noise on Individual Song Components.—The positive relationship between distance to the highway and average song duration could be because of traffic noise interrupting the songs of wrens singing near the highway; although this was not tested. Contrary to this, distance to ocean had a negative, albeit not significant, relationship with song duration. The difference in the direction of the effects could be because the wave frequency is longer than the traffic frequency, and therefore wrens can sing longer songs in between crashing waves. The absence of significant influence of highway noise on other song characteristics measured may have been because the traffic along Trans-Canada Highway 4 was not frequent or loud enough to cause the birds to adjust their songs more extensively. Many studies that have found significant impacts from traffic noise on bird song were evaluating busy highways carrying 30,000–50,000 vehicles/day (e.g., Rheindt 2003, Parris and Schneider 2009), compared to the highway in this study that carried many fewer vehicles/day during the peak period of Pacific Wrens singing and during the park's busiest month (unpubl. road count data, Pacific Rim National Park Reserve, 2011). It is also possible that vehicular speed contributed to the lack of significant influence of

highway noise on most wren song characteristics, since the posted speed limit is 80 km/h and this portion of the highway is meant as more of a scenic drive than a high-traffic commuting route. Finally, the peak in traffic is likely not overlapping with the maximum period of Pacific Wrens singing, which is at dawn. For these reasons, we do not interpret the general lack of effect of traffic noise on Pacific Wrens' songs as evidence that traffic noise does not influence bird song; instead, our results suggest that lower traffic volumes have less influence on bird songs than the well documented effects of high traffic volumes at other sites.

Future Studies.—Future studies could examine densities, pairing, and reproductive success of individuals found in noisy environments near the ocean. It is possible that despite adjustments to the songs and singing behavior of Pacific Wrens, the songs may not be sufficient for effective communication or may result in reduced attractiveness to females. A study of Ovenbirds (*Seiurus aurocapilla*) in two territories of varying noise levels but otherwise equal habitat quality found there were significantly more inexperienced first-year breeders and less pairing success in the noisy territories (Habib et al. 2007). It is also possible that these wrens changed their songs in ways that we did not measure. An additional avenue of research would be to examine whether Pacific Wrens adjust their vocal amplitude in the face of ocean and traffic noise. This phenomenon, known as the Lombard effect, is common in birds, humans, and monkeys (Junqua 1992, Brumm and Todt 2002, Brumm et al. 2004). Nemeth et al. (2013) found that increasing singing frequency was effective in mitigating acoustic masking but that the greatest effect came from the associated increase in amplitude.

ACKNOWLEDGMENTS

We thank the staff at Pacific Rim National Park Reserve, particularly Y. Zharikov, for logistical and field assistance. For funding, we thank the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation, the Government of Ontario, Parks Canada, Environment Canada's Science Horizons program, Symons Trust Fund for Canadian Studies, and the University of Windsor. We also thank two anonymous reviewers for valuable comments on the manuscript.

LITERATURE CITED

Bradbury, J. W. and S. L. Vehrencamp. 2011. Principles of animal communication. Second Edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434–440.

Brumm, H. and H. Slabbekoorn. 2005. Acoustic communication in noise. Advances in the Study of Behavior 35:151–209.

Brumm, H. and P. J. B. Slater. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behavioral Ecology and Sociobiology 60:475–481.

Brumm, H. and D. Todt. 2002. Noise-dependent song amplitude regulation in a territorial songbird. Animal Behavior 63:891–897.

Brumm, H., K. Voss, I. Kollmer, and D. Todt. 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. Journal of Experimental Biology 207:443–448.

Catchpole, C. K. and P. J. B. Slater. 2008. Bird song: biological themes and variations. Cambridge University Press, Cambridge, UK.

Chesser, R. T., R. C. Banks, F. K. Barker, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, Jr., J. V. Remsen, J. D. Rising, D. F. Stotz, and K. Winker. 2010. Fifty-first supplement to the American Ornithologists' Union check-list of North American birds. Auk 127:726–744.

Dabelsteen, T. and N. Mathevon. 2002. Why do songbirds sing intensively at dawn? A test of the acoustic transmission hypothesis. Acta Ethologica 4:65–72.

Douglas III, H. D. and W. E. Conner. 1999. Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. Naturwissenschaften 86:228–230.

Edwards, D. 2005. Pacific Rim National Park Reserve carnivore-human interaction research project report. Progress Report prepared for Pacific Rim National Park Reserve of Canada, Long Beach, USA.

Habib, L., E. M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of Ovenbirds *Seiurus aurocapilla.* Journal of Applied Ecology 44:176–184.

Halfwerk, W., S. Bot, J. Buikx, M. van der Velde, J. Komdeur, C. ten Cate, and H. Slabbekoorn. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences 108:14549–14554.

Hanna, D., G. Blouin-Demers, D. R. Wilson, and D. J. Mennill. 2011. Anthropogenic noise affects song structure in Red-winged Blackbirds (*Agelaius phoeniceus*). Journal of Experimental Biology 214:3549–3556.

Hu, Y. and G. C. Cardoso. 2010. Which birds adjust the frequency of vocalizations in urban noise? Animal Behavior 79:863–867.

Junqua, J. -C. 1992. The variability of speech produced in noise. Speech Processing in Adverse Conditions 43–52.

Lengagne, T., T. Aubin, J. Lauga, and P. Jouventin. 1999. How do King Penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? Proceedings of the Royal Society B 26:1623–1628.

MEDINA, L. AND C. D. FRANCIS. 2012. Environmental variability and acoustic signals: a multi-level approach in songbirds. Biology Letters 8:928–931.

MORTON, S. E. 1975. Ecological sources of selection on avian sounds. American Naturalist 109:17–34.

NEMETH, E. AND H. BRUMM. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Animal Behaviour 78:637–641.

NEMETH, E., N. PIERETTI, S. A. ZOLLINGER,, N. GEBER-ZAHN, J. PARTECKE, A. C. MIRANDA, AND H. BRUMM. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proceedings of the Royal Society B 280:1–7.

PARRIS, K. M. AND A. SCHNEIDER. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecology and Society 14:29.

PARRIS, K. M., M. VELIK-LORD, AND J. M. A. NORTH. 2009. Frogs call at a higher pitch in traffic noise. Ecology and Society 14:25.

POTVIN, D. A., K. M. PARRIS, AND R. A. MULDER. 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in Silvereyes (*Zosterops lateralis*). Proceedings of the Royal Society B 278:2464–2469.

QUINN, J. L., M. J. WHITTINGHAM, S. J. BUTLER, AND W. CRESSWELL. 2006. Noise, predation risk compensation and vigilance in the Chaffinch *Fringilla coelebs*. Journal of Avian Biology 37:601–608.

REIJNEN, R. AND R. FOPPEN. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. Journal of Applied Ecology 31:85–94.

R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RHEINDT, F. E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? Journal of Ornithology 144:295–306.

SLABBEKOORN, H. AND A. DEN BOER-VISSER. 2006. Cities change the songs of birds. Current Biology 16:2326–2331.

SLABBEKOORN, H. AND M. PEET. 2003. Ecology: birds sing at a higher pitch in urban noise. Nature 424:267–267.

SLABBEKOORN, H. AND E. A. RIPMEESTER. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17:72–83.

STATSOFT, INC. 2004. STATISTICA (data analysis software system). Version 7. Tulsa, Oklahoma, USA.

TOEWS, D. P. L. AND D. E. IRWIN. 2008. Cryptic speciation in a Holarctic passerine revealed by genetic and bioacoustic analyses. Molecular Ecology 17:2691–2705.

TOEWS, D. P. L. AND D. E. IRWIN. 2012. Pacific Wren (*Troglodytes pacificus*). The birds of North America. Number 720.

WILEY, R. H. AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology 3:69–94.

WOOD, W. E. AND S. M. YEZERINAC. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123:650–659.

ZAR, J. H. 2009. Biostatistical analysis. Fifth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

The Wilson Journal of Ornithology 126(2):279–287, 2014

REPRODUCTIVE SUCCESS AND HABITAT CHARACTERISTICS OF GOLDEN-WINGED WARBLERS IN HIGH-ELEVATION PASTURELANDS

KYLE R. ALDINGER[1,3] AND PETRA BOHALL WOOD[2]

ABSTRACT.—The Golden-winged Warbler (*Vermivora chrysoptera*) is one of the most rapidly declining vertebrate species in the Appalachian Mountains. It is the subject of extensive range-wide research and conservation action. However, little is known about this species' breeding ecology in high-elevation pasturelands, a breeding habitat with conservation potential considering the U.S. Natural Resource Conservation Service's Working Lands for Wildlife program targeting private lands in the Appalachian Mountains. We located 100 nests of Golden-winged Warblers in pastures in and around the Monongahela National Forest in West Virginia during 2008–2012. Daily nest survival rate (mean ± SE = 0.962 ± 0.006), clutch size (4.5 ± 0.1), and number of young fledged per nest attempt (2.0 ± 0.2) and successful nest (4.0 ± 0.1) fell within the range of values reported in other parts of the species' range and were not significantly affected by year or the presence/absence of cattle grazing. Classification tree analysis revealed that nests were in denser vegetation (≥52%) and closer to forest edges (<36.0 m) and shrubs (<7.0 cm) than random locations within the male's territory. Successful nests had significantly more woody cover (≥9%) within 1 m than failed nests. Our results suggest that cattle grazing at 1.2–2.4 ha of forage/animal unit with periodic mowing can create and maintain these characteristics without interfering with the nesting of Golden-winged Warblers. High-elevation pasturelands may provide a refuge for remaining populations of Golden-winged Warblers in this region. *Received 22 July 2013. Accepted 10 January 2014.*

Key words: breeding habitat, classification tree, Golden-winged Warbler, grazing, habitat selection, pasture, *Vermivora chrysoptera*.

The Golden-winged Warbler (*Vermivora chrysoptera*), a species being considered for Endangered Species Act listing, is one of the most rapidly declining birds in eastern North America (Sauer et al. 2012). The population in the Appalachian Mountains Bird Conservation Region (U.S. North American Bird Conservation Initiative Committee 2000) is declining more precipitously (North American Breeding Bird Survey, −8% per year [95% CI: −10, −7], Sauer et al. 2012) than the larger population in the upper Midwest, from which it likely is disjunct (Roth et al. 2012). In the Appalachian region, high elevation grazing lands may provide important breeding habitat for the species, in part because of reduced hybridization with Blue-winged Warblers (*V. cyanoptera*) at high elevations (>600 m; Welton 2003, Buehler et al. 2007). High elevation regions of West Virginia may be refuges for Golden-winged Warblers as Blue-winged Warblers have encroached on historic breeding sites at lower elevations (Canterbury et al. 1993, West Virginia Division of Natural Resources 2009).

Minelands (Bulluck and Buehler 2008, Patton et al. 2010, Bulluck et al. 2013) and timber harvests (Klaus and Buehler 2001, Kubel and Yahner 2008) are anthropogenic sources of habitat for Golden-winged Warblers previously studied in the Appalachians; however, abandoned and lightly grazed pasturelands have received little attention outside of informally published material (Wilson et al. 2007, Aldinger 2010). Golden-winged Warblers breed in private and public pasturelands in North Carolina (C. G. Smalling, pers. comm.), Virginia (L. P. Bulluck, pers. comm.), and West Virginia (Aldinger 2010). Across Golden-winged Warblers' breeding distribution in West Virginia (37,247 km^2, Roth et al. 2012), forest (82%) and grassland/pasture (9%) are the most abundant land cover types (Strager 2012). Of the 9% grassland/pasture, 429 km^2 are public land and 2,931 km^2 are private. On public lands like the Monongahela National Forest (MNF), relatively low stocking rates (1.2–2.4 ha of usable forage/animal unit [AU, defined as one bull or cow/calf pair], C. M. Johnson, pers. comm.) promote a long-term source of complex early successional habitat. Therefore, high-elevation pasturelands also may be important for Golden-winged Warblers because of their local

[1]West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, P. O. Box 6125, Morgantown, WV 26506, USA.
[2]U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, P. O. Box 6125, Morgantown, WV 26506, USA.
[3]Corresponding author; e-mail: kaldinge@mix.wvu.edu

abundance (Strager 2012, KRA, pers. obs.), especially given declining trends in farmland abandonment (Brown et al. 2005), their persistence as open shrubland habitat (Niering and Goodwin 1974), and their potential to simultaneously benefit both livestock and wildlife.

The peer-reviewed published literature lacks an in-depth investigation of Golden-winged Warblers' nesting habitat on cattle grazing lands. Such an investigation is needed to guide conservation actions and to test if cattle grazing can be a safe and effective management tool (Sutter and Ritchison 2005). This is particularly relevant because of opportunities to manage pasturelands under the Natural Resource Conservation Service's (NRCS) Working Lands for Wildlife program (Ciuzio et al. 2013). Our objectives were to quantify reproductive rates and habitat characteristics of Golden-winged Warblers nesting in pasturelands and to identify habitat characteristics indicative of successful and failed nests. We examined habitat at two spatial scales because breeding habitat selection can occur at multiple scales (Thogmartin 2010).

METHODS

Study Area.—During 25 April–1 July 2008–2012, we studied Golden-winged Warbler populations in nine pastures in or near the MNF in Randolph (38° 55′ 34″ N, 79° 44′ 52″ W) and Pocahontas (38° 19′ 05″ N, 80° 05′ 29″ W) counties, West Virginia, at elevations of 800–1,200 m. Pastures were 6–179 ha in size. Portions of seven pastures in the MNF had annual low intensity cattle grazing (1.2–2.4 ha of usable forage/AU during the grazing season of 15 May–1 Oct, C. M. Johnson, pers. comm.) and periodic mowing to create and maintain early successional habitat. A limited amount of nesting habitat, created by fencerow maintenance or historic grazing, was found outside but adjacent to these actively-grazed pastures. The eighth MNF pasture was abandoned in 1985. One of the MNF pastures had horses along with cattle. The ninth pasture was privately-owned and abandoned circa 1970 based on historic imagery and local knowledge (W. A. Tolin, pers. comm.). Because the pastures were in close proximity and generally stocked by the same few farmers, cattle grazing practices were consistent across pastures. Pastures had patchy and structurally complex vegetation, comprised of non-native pasture grasses, herbaceous vegetation, and shrub-scrub habitat primarily along the fenced edges and transitioning into surrounding tracts of intact hardwood forest (see results for common plant species).

Nest Monitoring.—During May–June each year, we followed methods for locating and monitoring nests as outlined in Martin and Geupel (1993) and Martin et al. (1997). Female behavior was carefully observed to discover nest locations, while taking care not to disturb nesting activity. We began monitoring nests after incubation was underway, because female Golden-winged Warblers may abandon nests if disturbed, especially during construction and egg-laying (Confer et al. 2003). We checked nests every 2–3 days initially and more frequently as fledging approached to maximize data precision while minimizing human disturbance to the nests. We noted whether or not the nest occurred in a location that was grazed during the concurrent nesting season.

We defined clutch size as the number of eggs present after the onset of incubation and number of young produced in each successful nest as the number of nestlings observed prior to fledging. A nest was considered successful if at least one chick fledged. We estimated daily survival rates (DSR) and evaluated models with year and the presence/absence of grazing as covariates using the nest survival model in program MARK (White and Burnham 1999) and Akaike's Information Criterion (AIC_c) as the model selection criterion (Burnham and Anderson 2002). Estimates of clutch size and number of young fledged were compared by year and presence/absence of grazing with analysis of variance (ANOVA) using package *stats* within the R Language and Environment for Statistical Computing Version 3.0.2 (R Development Core Team 2013). Annual sample sizes of nests were too small to simultaneously test year and presence/absence of grazing. We did not estimate seasonal fecundity because of difficulties in tracking all nesting behavior of individual females throughout the nesting season. Differences were considered statistically significant at $\alpha = 0.05$.

Vegetation Sampling.—We collected vegetation data within 1-m and 11.3-m radius plots at all nests and random locations between 6 June and 1 July during 2008–2012. By 6 June on our pastures, plants in each of our cover categories have reached full leaf development. To place random plots, we generated a random compass bearing (0–359°) and distance (25–50 m) from each nest. We used a stratified random distance to

ensure non-overlapping plots while remaining within the male's spot-mapped territory boundary. If the random plot fell outside of the male's spot-mapped territory or in non-nesting habitat (e.g., closed-canopy forest), we generated a new set of random numbers.

We sampled vegetation using a modified version of a standardized protocol developed for a collaborative nesting study of Golden-winged Warblers (Aldinger 2010, Roth et al. 2012). We measured height from the ground to the rim of the nest and recorded species and height of the substrate in which the nest was placed. Plant species or other substrates primarily responsible for concealing the nest were recorded. Six characteristics of the nearest non-blackberry/raspberry (*Rubus* spp.) shrub were recorded: species, height, average width, distance from the nest to the nearest branch and central stem (at 10 cm above the ground), and the number of stems at 10 cm above the ground. Within the 1-m radius plot, we visually estimated percent cover of grasses, forbs, litter, bare ground, *Rubus*, woody vegetation, and vines. Litter depth was measured in each cardinal direction 1 m from plot center. Basal area was measured from plot center using a 10-factor prism. Distance from plot center to forest edge, defined as a contiguous closed-canopy made up of trees >10 cm in diameter at breast height (dbh), was measured in the field or from aerial photographs. Elevation at plot center was measured from a 30-m resolution digital elevation model in ArcMap 10 (ESRI 2011). Within the 11.3-m radius plot, we counted the number of snags ≥2 m in height and ≥10 cm dbh. We estimated vegetation density by placing a board (2 m tall, 40 cm wide) on the ground 10 m from plot center in each of the four cardinal directions and recorded how many of the twenty 20-cm squares were <50% visible when standing at plot center. Across the 11.3-m radius plot, we visually estimated average height of the shrub and sapling layer. We also measured percent cover of grasses, forbs, vines, *Rubus*, shrubs, saplings (1–10 cm dbh and ≥1 m in height), and canopy trees (>10 cm dbh) based on ocular tube "hits" (James and Shugart 1970) at five points along 11.3-m transects radiating from plot center in each cardinal direction. Observers recorded whether each cover type intersected the ocular tube crosshairs when viewing through the ocular tube straight towards the ground and straight up. For all vegetation data, analyses, results, and interpretations, *Rubus* was considered separately from shrubs and woody plants.

Classification Tree Analysis.—We used recursive partitioning (classification trees, CTs), a robust nonparametric technique (De'ath and Fabricius 2000), to identify habitat characteristics that distinguished nests from random plots and successful from unsuccessful nests (Dellinger et al. 2007). We chose this technique because little was known about Golden-winged Warblers' breeding habitat in active cattle pastures, particularly, how grazing may influence vegetation structure and development. CTs can reveal complex data structure (Vaysseires et al. 2000) and serve as the basis for investigating future hypotheses. The experimental unit was each individual nest or random plot and all data were used for model-building. CT analyses were completed using package *mvpart* within the R Language and Environment for Statistical Computing Version 3.0.2 (R Development Core Team 2013).

We ran a series of 50 10-fold cross validations (CV) and selected the final CT size using the 1-SE rule (De'ath and Fabricius 2000), where the smallest CT with an estimated error within one standard error of the minimum CV error is considered the best tree. This decision rule results in smaller CTs, with minimal increase in the estimated error rate over the minimum CV error (at most <1-SE, De'ath and Fabricius 2000), that are better-suited for prediction. CV classification accuracy (±95% confidence intervals, Tan et al. 2006), which is a better indicator of true accuracy than model accuracy (De'ath 2002), and CV error were used to evaluate CT performance. CV error ranges from zero for perfect classification to close to one for random classification; the value can exceed one if classification is worse than random (De'ath 2002). Cohen's Kappa (Cohen 1960) is an analogue of 1 – CV error, so we qualitatively evaluated CT performance using guidelines in Landis and Koch (1977; 1 – CV error <0.00 = poor agreement, 0.01–0.20 = slight, 0.21–0.40 = fair, 0.41–0.60 = moderate, 0.61–0.80 = substantial, 0.81–1.00 = almost perfect). All variables retained in the CTs comparing nests and random plots were tested for differences using the nonparametric Wilcoxon signed-rank, because both plots were within the male's territory. All variables retained in the CTs comparing successful and failed nests were tested for differences using the Wilcoxon rank sum test (Zar 2010).

TABLE 1. Variables measured in Golden-winged Warblers' breeding habitat during 2008–2012 in Randolph and Pocahontas counties, West Virginia. Variables retained in CTs are bold. Nest-scale variables were those collected within 1 m of plot center, first egg date, and measurements of the nearest shrub. Plot-scale variables were those collected across the 11.3 m plot and larger.

	Nest (n = 100)		Random (n = 100)		Successful nest (n = 39)		Failed nest (n = 43)	
Variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Nest-scale[a]								
Litter cover (%)	3.8	0.7	10.0	1.5	4.7	1.2	2.1	0.4
Grass cover (%)	20.7	1.4	25.6	2.0	19.2	1.8	22.4	2.6
Bare cover (%)	1.3	0.2	5.1	1.1	1.5	0.4	1.0	0.4
Forb cover (%)	41.5	1.8	38.8	2.0	40.1	2.9	40.6	2.7
Woody cover (%)	14.2	1.7	8.6	1.3	**16.6**	**2.6**	**12.6**	**2.9**
Vine cover (%)	2.3	0.6	2.4	0.7	1.5	0.6	3.1	1.2
Rubus cover (%)	16.3	1.9	9.7	1.7	16.4	3.4	18.2	2.8
Litter depth (cm)	2.7	0.1	2.6	0.3	2.5	0.2	2.8	0.2
Dist. to nearest shrub stem (cm)	**87.0**	**14.1**	**149.5**	**19.0**	57.4	14.8	102.1	18.6
Dist. to nearest shrub branch (cm)	47.7	10.9	88.4	15.8	25.4	9.3	51.3	11.4
Shrub height (cm)	159.1	11.8	187.1	17.7	169.3	21.7	153.5	16.5
Shrub width (cm)	119.5	14.3	171.0	20.9	129.6	26.0	115.3	21.8
No. of shrub stems at 10 cm	2.5	0.3	2.3	0.2	2.7	0.6	2.3	0.3
Height to nest rim (cm)	12.5[b]	0.4			12.1	0.5	12.9	0.6
Substrate height (cm)	89.0	2.8			91.6	4.4	87.3	4.3
Julian first egg date	139.2[c]	0.9			137.9	1.1	141.2[d]	1.5
Plot-scale								
Grazed during nesting season (%)	73.0		76.0		74.4		76.7	
Grass cover (%)	69.8	2.5	69.2	2.8	72.6	3.8	69.4	3.9
Forb cover (%)	83.7	1.6	79.7	2.0	85.1	2.1	82.4	2.9
Vine cover (%)	8.8	1.6	9.8	2.1	7.4	2.0	10.6	3.0
Rubus cover (%)	27.3	2.4	21.0	2.2	**25.0**	**3.8**	**31.4**	**3.3**
Shrub cover (%)	45.6	2.0	38.1	2.2	47.1	3.0	43.0	3.0
Sapling cover (%)	9.1	1.2	8.3	1.4	8.8	2.0	9.8	1.9
Canopy cover (%)	12.2	1.6	9.1	1.6	11.0	2.3	10.8	2.7
Elevation (m)	950.2	8.6	951.9	8.7	952.3	13.0	949.5	13.8
Basal area (m^2/ha)	3.6	0.4	3.9	0.5	2.9	0.6	4.2	0.7
Snags (No./11.3-m radius)	0.1	0.0	0.1	0.0	0.2	0.1	0.1	0.0
Dist. to forest edge (m)	**28.9**	**2.4**	**37.0**	**2.4**	28.1	3.0	34.5	4.7
Vegetation density (%)	**73.7**	**1.9**	**64.7**	**2.5**	72.7	2.8	76.0	2.8
Sapling layer height (m)	3.3	0.2	2.8	0.2	3.7	0.4	3.0	0.3
Shrub layer height (m)	3.1	0.1	3.0	0.1	3.3	0.2	3.0	0.1

[a] Nest-scale also included *nearest shrub species*.
[b] n = 97, three damaged nests could not be measured.
[c] n = 93, first egg dates could not be reliably estimated for seven nests.
[d] n = 36, first egg dates could not be reliably estimated for seven nests.

Breeding habitat selection occurs at multiple spatial scales in Golden-winged Warblers (Thogmartin 2010), so explanatory variables were organized into two spatial scales: nest-scale (variables collected within 1 m of plot center, first egg date, and measurements of the nearest shrub) and plot-scale (variables collected across the 11.3 m plot and larger; see Table 1 for a list of variables and their respective scales). We combined all variables in a global CT to test if nest site selection or nest survival were influenced by both nest- and plot-scale variables.

RESULTS

Nest Habitat.—We located and measured habitat characteristics (Table 1) at 100 nests of Golden-winged Warblers during 2008–2012 (range 7–30 nests/year). The majority were found during construction (65%), followed by incubation (18%), brooding (10%), and egg-laying (7%). Twenty-one plant species, typically those with firm stems, served as primary nest substrates; 93% of nests were supported by *Rubus*, goldenrod, and/or other woody shrub stems. Of the seven plant species recorded as the nearest shrub stem at

TABLE 2. Survival of Golden-winged Warblers' nests by year and presence/absence of cattle grazing during 2008–2012 in Randolph and Pocahontas counties, West Virginia.

Year	Nest survival				
	DSR	SE	95% CI	Nest survival[a]	*n*
2008	0.972	0.020	0.894–0.993	0.508	6
2009	0.971	0.012	0.936–0.987	0.496	13
2010	0.963	0.012	0.932–0.980	0.412	20
2011	0.960	0.010	0.934–0.976	0.387	24
2012	0.952	0.014	0.915–0.973	0.313	19
	Cattle grazing during the nesting season				
Grazed	0.963	0.006	0.948–0.973	0.408	62
Not grazed	0.959	0.013	0.925–0.978	0.374	20
Overall	0.962	0.006	0.949–0.972	0.400	82

[a] Probability of surviving a 23.5-day nesting period (mean nesting period length from laying of the first egg to fledging in our study).

nest and random plots, hawthorn (*Crataegus* spp.) occurred most frequently (nests 56%; random plots 55%). All nests were built at a micro-edge between dense vegetation and an herbaceous opening, including fencerows, cattle trails, browse lines, and recently mowed strips. Dominant plant species at nests in each of the seven plot-scale cover categories (Table 1) included sweet vernal-grass (*Anthoxanthum odoratum*; 78% of nests), goldenrod (95%), devil's darning needles (*Clematis virginiana*; 45%), *Rubus* (89%), hawthorn (97%), black locust (*Robinia pseudoacacia*) saplings (30%), and black locust canopy trees (19%).

Reproductive Success.—Thirty-nine nests were successful, 38 depredated, 17 failed before observed with eggs laid (14 of which were partially-built/first-attempt nests before 21 May), 3 abandoned during egg-laying, 2 sterile, and 1 undetermined for a total of 1,105 exposure days across a 53-day breeding season (earliest egg laid 7 May, latest fledgling 27 Jun, latest nest failed 28 Jun). For nest survival analyses, we included the 82 nests that reached at least egg-laying. No nests were trampled by cattle and cattle grazing during the nesting season did not influence nest placement (Table 1). There was no double-brooding, but females frequently re-nested after failed nest attempts. One female attempted three nests in one breeding season. No nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*); although using the high count across two visits of 10-min, 100-m radius point counts we detected 0.6 ± 0.1 (mean ± SE) cowbirds per point and cowbirds occurred on 40.5 ± 4.7% of points annually (KRA, unpubl. data).

Using the nest survival model in program MARK, the constant survival model received the most support (AIC_c weight [w_i] = 0.71), the presence/absence of grazing model had some support (ΔAIC_c = 1.94, w_i = 0.27), and year had no support (ΔAIC = 6.78, w_i = 0.02). Beta coefficient confidence intervals for each year and presence/absence of grazing overlapped zero, indicating that these variables had little influence on nest survival. Assuming that females re-nest one time after nest failure, overall probability of a female successfully fledging young was 64% ($1 - [1–0.40]^2 = 0.64$; Table 2). Complete clutch size, number of fledglings/nest attempt, and number of fledglings/successful nest also were each similar across years and the presence/absence of cattle grazing (Table 3).

Nests Versus Random Plots.—At the nest-scale, distance to the nearest shrub stem was the only variable that distinguished nests (<7 cm from a shrub stem) from random locations (≥7 cm, Table 4). The mean distance away from a shrub stem for random plots was almost twice that of nests (Table 1) and differed significantly (Table 4). The global CT selected using the 1-SE rule was equal to the nest-scale CT.

At the plot-scale, vegetation density was greater at nests and distance to forest edge was greater at random locations (Table 1); both differed significantly between nests and random locations (Table 4). Accuracy of the nest-scale and plot-scale CTs was similar (~70%, Table 4) and both performed moderately (1 – CV error = 0.40–0.60).

Successful Versus Failed Nests.—CTs used to distinguish successful and failed nests had lower CV accuracy than CTs comparing nests and random plots. CT performance was poor at both

TABLE 3. Reproductive rates of Golden-winged Warblers by year and presence/absence of cattle grazing during 2008–2012 in Randolph and Pocahontas counties, West Virginia.

	Complete clutch size (# eggs)			Young fledged/nest attempt			Young fledged/successful nest		
Year	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
2008	4.6	0.2	5	2.5	0.9	6	3.8	0.6	4
2009	4.3	0.2	11	2.2	0.6	13	4.1	0.3	7
2010	4.5	0.1	15	2.0	0.5	20	4.0	0.3	10
2011	4.8	0.2	20	1.6	0.4	24	3.8	0.5	10
2012	4.5	0.2	17	1.7	0.5	18	4.4	0.4	7
ANOVA	$F_{4,62} = 0.70$, $P = 0.59$			$F_{4,75} = 0.35$, $P = 0.85$			$F_{4,32} = 0.40$, $P = 0.81$		
	Cattle grazing during the nesting season								
Grazed	4.6	0.1	52	1.9	0.3	61	4.2	0.2	28
Ungrazed	4.5	0.2	16	1.8	0.5	20	3.5	0.5	10
ANOVA	$F_{1,62} = 0.02$, $P = 0.89$			$F_{1,71} = 0.52$, $P = 0.47$			$F_{1,32} = 2.81$, $P = 0.10$		
Overall	4.5	0.1	68	2.0	0.2	81	4.0	0.1	38

nest and plot scales (1 – CV error < 0.00). At the nest-scale, woody cover was the only variable that distinguished successful from failed nests, although CV accuracy was 50% (Table 4). The Wilcoxon rank sum test did show that successful nests had significantly more woody cover than failed nests though (Table 1). The global CT was equal to the nest-scale CT.

The plot-scale CT used *Rubus* cover to partition successful (<18%) from failed (≥18%) nests, but CV accuracy was only 40% (Table 4). *Rubus* cover did not differ between successful and failed nests based on the Wilcoxon rank sum test.

DISCUSSION

Throughout Golden-winged Warblers' range, nesting habitat is described as a complex patchy mosaic of herbaceous vegetation interspersed with *Rubus*, shrubs, and young trees of varying heights adjacent to a forested edge (Confer et al. 2011, Roth et al. 2012). Nest sites are characterized by micro-edges with high amounts of herbaceous cover and rigid stems to support the nest (Bulluck and Buehler 2008, Confer et al. 2011, Roth et al. 2012). In high elevation pasturelands in our study, Golden-winged Warblers primarily used certain nest- (proximity to shrubs) and plot-scale (vegetation density and proximity to forest edge) habitat features when selecting nest sites. Thus, Golden-winged Warblers breeding in this previously unstudied habitat in West Virginia used features similar to those used in other habitat types, including regenerating aspen (*Populus* spp.) clearcuts (Roth and Lutz 2004), reclaimed surface mines (Bulluck and Buehler 2008, Patton et al. 2010, Bulluck et al. 2013), wetlands (Rossell et al. 2003), and utility rights-of-way (Kubel and Yahner 2008).

Nest survival, clutch size, and the number of host and Brown-headed Cowbird young fledged, fell within the range of values reported across Golden-winged Warblers' range (Will 1986,

TABLE 4. Summary statistics for classification tree analyses. Global scale models were identical to their respective nest-scale models.

Scale	CV accuracy (95% CI)	CV error	Variables	Tree structure	Wilcoxon test p-value
			Nest versus random		
Nest	70.7 (64.0–76.6)	0.587	Distance from nest to nearest shrub stem (cm)	<7.0 = nest	<0.001
Plot[a]	70.3 (63.6–76.2)	0.594	Vegetation density (%)	≥51.9 = nest	0.003
			Distance to forest edge (m)	<36.0 = nest	<0.001
			Successful versus failed nests		
Nest	49.5 (38.9–60.1)	1.060	Woody cover (%)	≥8.5 = successful	0.035
Plot	40.2 (30.3–51.0)	1.160	*Rubus* cover (%)	<17.5 = successful	0.11

[a] If vegetation density is ≥51.9% and distance to forest edge is <36 m, then classify as nest.

Klaus and Buehler 2001, Confer et al. 2003, Reed et al. 2007, Bulluck and Buehler 2008, Kubel and Yahner 2008, Confer et al. 2010, Bulluck et al. 2013, Streby and Andersen 2013). Our nest survival estimate (40%) was within 10% of similarly derived estimates from geographic extremes of the breeding distribution (49% in Tennessee, 33% in Ontario, Bulluck et al. 2013; 50% in Minnesota, Streby and Andersen 2013). In these studies and across their breeding distribution, Golden-winged Warblers rely extensively on anthropogenic habitats like abandoned farmlands, reclaimed mines, and timber harvests. Some anthropogenic habitats could jeopardize population persistence because of low nest productivity (e.g., narrow utility rights-of-way, Kubel and Yahner 2008). However, the pastures we studied appeared to provide productive nesting habitat despite the ongoing anthropogenic influence. Nest parasitism by Brown-headed Cowbirds has been documented in 15–35% of Golden-winged Warblers' nests in some areas (Will 1986, Coker and Confer 1990, Confer et al. 2003, Kubel and Yahner 2008, Confer et al. 2011), and cowbirds are associated with livestock and agricultural habitats in the central Appalachians (Gates and Evans 1998), but we observed no parasitism during this study. Based on this comparison with other studies, low-intensity cattle grazing in high-elevation pasturelands can create and maintain productive habitat for Golden-winged Warblers.

Application of our results largely depends on habitat management on private lands (Ciuzio et al. 2013), which can be accomplished through projects like the NRCS Working Lands for Wildlife program. West Virginia leads the nation in the proportion of its farms classified as small (98% had ≤$250,000 in sales of agricultural commodities/year) and family-owned (95%, National Agricultural Statistics Service [NASS] 2013). West Virginia counties within the Golden-winged Warblers' breeding distribution (Roth et al. 2012) contained a total of 2,345 km^2 of permanent pasture in 2013 (NASS 2013). These counties (n = 24) averaged 1 ha of pasture/head of cattle (range 0.7–1.7 ha/head, NASS 2013). The NASS (2013) estimates consider a cow/calf pair as two head, so their estimates actually are more similar to the recommended stocking rate on the MNF (1.2–2.4 ha/AU), which considers a cow/calf pair as one AU. Pastures near our study areas with higher stocking rates or appropriate stocking rates but with more frequent mowing generally were not suitable for nesting of Golden-winged Warblers, particularly if there were no browse resistant woody plants (e.g., hawthorn) already established (KRA, pers. obs.).

CT models identified two habitat variables that differentiated between successful and failed nests, but the poor model performance suggests that nest predation of Golden-winged Warblers may be a random process (Bulluck and Buehler 2008) in these pastures. However, when we followed CT analysis with the Wilcoxon rank sum test, successful nests did have significantly greater nest-scale woody cover than failed nests. Bulluck and Buehler (2008) similarly found that nest predation of Golden-winged Warblers may be a random process but that nests with a woody stem in the substrate had marginally lower survival. Fine-scale woody vegetation likely is influencing the placement and fate of nests and warrants further study and attention by managers. Investigating woody plant metrics other than presence/absence and percent cover may better elucidate the relationship.

Blue-winged Warblers have replaced Golden-winged Warblers throughout most of West Virginia (Canterbury et al. 1993, West Virginia Division of Natural Resources 2009). However, during 5 years of our study on the pastures, just 3% (n = 30) of male Golden-winged Warblers' phenotypes showed mitochondrial DNA introgression (L. M. Stenzler, Cornell Laboratory of Ornithology, unpubl. data) and 25 of 178 *Vermivora* spp. territories involved a non-Golden-winged Warbler phenotype (KRA, unpubl. data). Fifteen of these 25 territories involved a Golden-winged Warbler's phenotype paired with a non-Golden-winged Warbler's phenotype. Although relatively uncommon, Blue-winged Warblers or hybrids that colonized and successfully mated often did so with a Golden-winged Warbler because of the lack of conspecific mates. Thus, colonization by non-Golden-winged Warblers can have immediate and compounding effects on genetic recruitment. Limiting hybridization and competition through managing habitats and habitat characteristics selected by Golden-winged Warblers may be critical for persistence of the species in the Appalachian region (Patton et al. 2010). We have identified manageable characteristics to guide conservation actions in the central Appalachians, where high-elevation pasturelands may provide a refuge for remnant populations of this species.

ACKNOWLEDGMENTS

Funding for this project was granted by the WV Division of Natural Resources Wildlife Diversity Program, U.S. Fish and Wildlife Service Migratory Bird Program, U.S. Forest Service Monongahela National Forest, U.S. Natural Resource Conservation Service, and the National Fish and Wildlife Foundation. Logistic and administrative support was provided by the USGS West Virginia Cooperative Fish and Wildlife Unit and the Division of Forestry and Natural Resources at West Virginia University. The WVDNR Elkins Operation Center and the Littlefield family provided housing and the USFS allowed access to the study sites. We thank A. Dalton, M. Frantz, C. Fitzmorris, J. Kreiser, C. Lauzau, A. Newman, V. Olmstead, K. Pratt, J. Riffle, M. Roach, C. Roy, C. Sedgwick, L. Smith, L. Stout, D. Ware, and M. Weston for their long hours of work in the field. Members of the Golden-winged Warbler Working Group provided valuable insight for this project and manuscript. G. Merovich aided in data analyses. This study was completed under the auspices of West Virginia University IACUC protocols 07-0303 and 10-0201. Use of tradenames does not imply endorsement by the Federal Government.

LITERATURE CITED

ALDINGER, K. R. 2010. Playback surveys and breeding habitat characteristics of Golden-winged Warblers (*Vermivora chrysoptera*) on high-elevation pasturelands on the Monongahela National Forest, West Virginia. Thesis, West Virginia University, Morgantown, USA.

BROWN, D. G., K. M. JOHNSON, T. R. LOVELAND, AND D. M. THEOBALD. 2005. Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15:1851–1863.

BUEHLER, D. A., A. M. ROTH, R. VALLENDER, T. C. WILL, J. L. CONFER, R. A. CANTERBURY, S. B. SWARTHOUT, K. V. ROSENBERG, AND L. P. BULLUCK. 2007. Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. Auk 124:1439–1445.

BULLUCK, L. P. AND D. A. BUEHLER. 2008. Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. Auk 125:551–559.

BULLUCK, L. P., D. A. BUEHLER, R. VALLENDER, AND R. J. ROBERTSON. 2013. Demographic comparison of Golden-winged Warbler (*Vermivora chrysoptera*) populations in northern and southern extremes of their breeding range. Wilson Journal of Ornithology 125:479–490.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach. Fifth Edition. Springer-Verlag, New York, New York, USA.

CANTERBURY, R. A., D. M. STOVER, AND T. C. NELSON. 1993. Golden-winged Warblers in southern West Virginia: status and population ecology. Redstart 60:97–106.

CIUZIO, E., W. L. HOHMAN, B. MARTIN, M. D. SMITH, S. STEPHENS, A. M. STRONG, AND T. VERCAUTEREN. 2013. Opportunities and challenges to implementing bird conservation on private lands. Wildlife Society Bulletin 37:267–277.

COHEN, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20:37–46.

COKER, D. R. AND J. L. CONFER. 1990. Brown-headed Cowbird parasitism on Golden-winged and Blue-winged warblers. Wilson Bulletin 102:550–552.

CONFER. J. L, K. W. BARNES, AND E. C. ALVEY. 2010. Golden- and Blue-winged warblers: distribution, nesting success, and genetic differences in two habitats. Wilson Journal of Ornithology 122:273–278.

CONFER, J. L., P. HARTMAN, AND A. ROTH. 2011. Golden-winged Warbler (*Vermivora chrysoptera*). The birds of North America. Number 20.

CONFER, J. L., J. L. LARKIN, AND P. E. ALLEN. 2003. Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. Auk 120:138–144.

DE'ATH, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. Ecology 83:1105–1117.

DE'ATH, G. AND K. A. FABRICIUS. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

DELLINGER, R. L., P. B. WOOD, P. D. KEYSER, AND G. SEIDEL. 2007. Habitat partitioning of four sympatric thrush species at three spatial scales on a managed forest in West Virginia. Auk 124:1425–1438.

ESRI. 2011. ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

GATES, J. E. AND D. R. EVANS. 1998. Cowbirds breeding in the central Appalachians: spatial and temporal patterns in habitat selection. Ecological Applications 8:27–40.

JAMES, F. C. AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

KLAUS, N. A. AND D. A. BUEHLER. 2001. Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. Wilson Bulletin 113:297–301.

KUBEL, J. E. AND R. H. YAHNER. 2008. Quality of anthropogenic habitat for Golden-winged Warblers in central Pennsylvania. Wilson Journal of Ornithology 120:801–812.

LANDIS, J. R. AND G. G. KOCH. 1977. The measurement of observer agreement for categorical data. Biometrics 33:159–174.

MARTIN, T. E., C. J. CONWAY, W. M. HOCHACHAKA, P. ALLEN, AND W. JENKINS. 1997. BBIRD field protocols. U.S.G.S. Biological Resources Division, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA. www.umt.edu/bbird/protocol/veg.aspx (accessed 1 Apr 2013).

MARTIN, T. E. AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

NIERING, W. A. AND R. H. GOODWIN. 1974. Creation of relatively stable shrublands with herbicides: arresting

"succession" on rights-of-way and pastureland. Ecology 55:784–795.

PATTON, L. L., D. S. MAEHR, J. E. DUCHAMP, S. FEI, J. W. GASSETT, AND J. L. LARKIN. 2010. Do the Golden-winged Warbler and Blue-winged Warbler exhibit species-specific differences in their breeding habitat use? Avian Conservation and Ecology 5:2.

R DEVELOPMENT CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ROTH, A. M., R. W. ROHRBAUGH, T. WILL, AND D. A. BUEHLER (Editors). 2012. Golden-winged Warbler status review and conservation plan. www.gwwa.org/plan (accessed 7 Jul 2013).

SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI, JR., AND W. A. LINK. 2012. The North American Breeding Bird Survey, results and analysis 1966–2011. Version 07.03.2013 USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/bbs.html (accessed 16 Dec 2013).

STRAGER, M. P. 2012. Landuse/Landcover of West Virginia (2011). West Virginia GIS Technical Center, West Virginia University, Morgantown, USA. wvgis.wvu.edu/data/dataset.php?ID=451 (accessed 5 Dec 2013).

STREBY, H. M. AND D. E. ANDERSEN. 2013. Testing common assumptions in studies of songbird nest success. Ibis 155:327–337.

SUTTER, B. AND G. RITCHISON. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. Journal of Field Ornithology 76:345–351.

TAN, P. N., M. STEINBACH, AND V. KUMAR. 2006. Introduction to data mining. Pearson, Boston, Massachusetts, USA.

THOGMARTIN, W. E. 2010. Modeling and mapping Golden-winged Warbler abundance to improve regional conservation strategies. Avian Conservation and Ecology 5:12.

U.S. NORTH AMERICAN BIRD CONSERVATION INITIATIVE COMMITTEE. 2000. North American bird conservation initiative: bird conservation region descriptions. U.S. Fish and Wildlife Service, Division of Bird Habitat Conservation, Washington, DC, USA.

U.S. NATIONAL AGRICULTURAL STATISTICS SERVICE. 2013. West Virginia agricultural statistics. Bulletin number 44. www.nass.usda.gov/Statistics_by_State/West_Virginia/Publications/Annual_Statistical_Bulletin (accessed 18 Dec 2013).

VAYSSEIRES, M. P., R. E. PLANT, AND B. H. ALLEN-DIAZ. 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11:679–694.

WELTON, M. 2003. Status and distribution of the Golden-winged Warbler in Tennessee. Migrant 74:61–82.

WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46:120–139.

WILSON, M. D., B. D. WATTS, M. G. SMITH, J. P. BREDLAU, AND L. W. SEAL. 2007. Status assessment of Golden-winged Warblers and Bewick's Wrens in Virginia. Center for Conservation Biology Technical Report Series, CCBTR-07-02. College of William and Mary, Williamsburg, Virginia, USA.

WEST VIRGINIA DIVISION OF NATURAL RESOURCES. 2009. West Virginia Breeding Bird Atlas II. bird.atlasing.org/Atlas/WV/Main?viewResults=1 (accessed 9 Dec 2013).

ZAR, J. H. 2010. Biostatistical analysis. Fifth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

The Wilson Journal of Ornithology 126(2):288–297, 2014

SELECTION OF FOREST CANOPY GAPS BY MALE CERULEAN WARBLERS IN WEST VIRGINIA

KELLY A. PERKINS[1,3,4] AND PETRA BOHALL WOOD[2]

ABSTRACT.—Forest openings, or canopy gaps, are an important resource for many forest songbirds, such as Cerulean Warblers (*Setophaga cerulea*). We examined canopy gap selection by this declining species to determine if male Cerulean Warblers selected particular sizes, vegetative heights, or types of gaps. We tested whether these parameters differed among territories, territory core areas, and randomly-placed sample plots. We used enhanced territory mapping techniques (burst sampling) to define habitat use within the territory. Canopy gap densities were higher within core areas of territories than within territories or random plots, indicating that Cerulean Warblers selected habitat within their territories with the highest gap densities. Selection of regenerating gaps with woody vegetation >12 m within the gap, and canopy heights >24 m surrounding the gap, occurred within territory core areas. These findings differed between two sites indicating that gap selection may vary based on forest structure. Differences were also found regarding the placement of territories with respect to gaps. Larger gaps, such as wildlife food plots, were located on the periphery of territories more often than other types and sizes of gaps, while smaller gaps, such as treefalls, were located within territory boundaries more often than expected. The creations of smaller canopy gaps, <100 m^2, within dense stands are likely compatible with forest management for this species. *Received 2 May 2013. Accepted 7 December 2013.*

Key words: canopy gaps, Cerulean Warbler, kernel home range, *Setophaga cerulea*, territory size, vegetation structure.

Cerulean Warblers (*Setophaga cerulea*) have declined ~75% since 1966 (Sauer et al. 2011), and habitat loss and degradation are thought to be contributing factors (Hamel et al. 2004). Although the Cerulean Warbler (hereafter, cerulean) is classified as an area-sensitive species adapted to large unfragmented blocks of mature forest (Buehler et al. 2013), interior canopy gaps appear to be an important habitat component (Oliarnyk and Robertson 1996, Jones and Robertson 2001, Bosworth 2003, Weakland and Wood 2005, Wood et al. 2006, Roth and Islam 2008). However, despite Hamel (2000: 65) identifying research that examines the preferred vegetative structure, including the "vertical distribution of vegetation and the horizontal distribution of canopy gaps" as a high priority need for this species, the selection of canopy gaps by ceruleans has not been evaluated explicitly, although a few studies have addressed the use of canopy gaps by ceruleans peripherally. Oliarnyk and Robertson (1996) documented that nest sites frequently were within 30 m of a canopy gap in Ontario. Several studies have found that ceruleans were positively associated with snags (Bosworth 2003, Weakland and Wood 2005, Carpenter et al. 2011), likely because of the attractiveness of small canopy openings and not the snag itself. However, other studies have provided evidence that gap use does not differ from availability, or have had ambiguous results. Carpenter et al. (2011) found plots used by ceruleans had larger canopy gaps than unused plots, and cerulean presence was related to decreasing distances to the nearest gap. However, a principal component analysis in the same paper disassociated presence with distance to canopy gaps and their size. Also, Barg et al. (2006) found proximity of cerulean locations to gaps did not differ from random and that nest success was reduced as nests were placed closer to gaps. Adding to this ambiguity, few papers provided their definition of a canopy gap, or the methods used to identify them in the field, so it is difficult to compare findings among them. Further, since ceruleans spend most of their time in the forest canopy (Wood and Perkins 2012, Buehler et al. 2013), gaps in the mid- and upper-canopy that existed above a lower canopy or sub canopy strata may be important to them and it is unknown whether these gaps were included in previous studies. This is the first study to quantify and test Cerulean Warbler selection of canopy gaps within territories according to their vegetative structure and size.

The utility that canopy gaps may provide to forest birds and ceruleans has not been conclusively

[1] West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, 313 Percival Hall, P. O. Box 6125, Morgantown, WV 26506, USA.

[2] U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, 313 Percival Hall, P. O. Box 6125, Morgantown, WV 26506, USA; pbwood@wvu.edu

[3] Current address: New York Natural Heritage Program, 625 Broadway 5th Floor, Albany, NY 12233, USA.

[4] Corresponding author; e-mail: kaperkin@esf.edu

studied and there may be multiple benefits. Canopy gaps may be attractive as a warm location to sing during cold mornings, as territory boundaries (Perkins 2006), or to increase visibility and song projection (Smith and Dallman 1996, Barg et al. 2006). Insect abundance may be higher in gaps (Blake and Hoppes 1986, Smith and Dallman 1996, Gorham 2002), so they may provide greater foraging opportunities (Smith and Dallman 1996). Potentially, characteristics of the gap such as size, vegetative structure (e.g., height of the surrounding canopy and the vegetation within it), or the type of gap (e.g., whether it is an autogenic treefall or a mowed field) could influence its utility and attractiveness to ceruleans.

The objective of our study was to quantify the types, sizes, and vegetative structure of canopy gaps used by male ceruleans, and we tested three hypotheses related to this: 1) selection of gaps included within territories and territory core areas (50% kernel density estimates) varies by the type, size, and vegetative structure of the gap; 2) gap type and size differ between gaps located within or on the periphery of the territories; and 3) the density of gaps within core areas and territories, as well as the proportion of the territory or core area covered by gaps, differs from random.

METHODS

Study Area.—The study was conducted on Lewis Wetzel Wildlife Management Area near Jacksonburg, in Wetzel County, WV. The surrounding landscape was extensively forested with >90% forest cover in a 10-km radius at the time of the study. Lewis Wetzel Wildlife Management Area (39° 29′ 01″ N, 80° 37′ 07″ W) was 5,418 ha with elevations of 224–476 m. It was predominantly mature forest except for three clearcuts harvested in 1996 and 1997. We conducted the study on two ridgetop sites that differed in species composition, forest structure, and land use history. The area we surveyed on Snake Ridge (SR) was ~44.5 ha and was located along 1.9 km of the ridgetop. It was a xeric, mature forest of chestnut oaks (*Quercus montana*) and scarlet oaks (*Q. coccinea*) with no recent anthropogenic disturbances. Canopy gaps on SR consisted only of autogenic treefall gaps. The site on Hart Ridge (HR) was ~30 ha along 1.6 km of ridgetop. It was a second-growth, mesic forest of sugar maple (*Acer saccharum*), red maple (*A. rubrum*), tuliptree (*Liriodendron tulipifera*), black locust (*Robinia pseudoacacia*), and hickory (*Carya* spp.) that had formerly been farmed and grazed. It had more variety in the types of canopy disturbances. Besides treefall gaps, HR had a trail running along the ridgetop, which created intermittent canopy openings, and 3 managed wildlife openings 0.17–0.32 ha in size. The forest on HR may be typical of other young mixed mesophytic forests with similar land use histories that are common throughout the Appalachian region. The chestnut oak-scarlet oak forest on SR is a community type found on xeric, rocky ridgetops that are also present throughout the Appalachian region. Both sites had moderate to high relative abundance of ceruleans. Estimates from point counts conducted in 2004 along each ridgetop were 1.1 ceruleans/point on SR (n = 9 points) and 2.0 ceruleans/point on HR (n = 11 points).

Cerulean Warbler Surveys.—In mid-May through the end of June 2005, we intensively sampled territories of ceruleans at two sites, as well as randomly-placed sample plots, to understand selection of forest canopy gaps by comparing territories with available habitat. Following methods from Barg et al. (2005), we collected locations in sampling bursts to maximize the number of points taken over a short period. For each sampling burst, a male cerulean was followed for 30 mins every 3–5 days between 0530 and 1030 Eastern Daylight Time (EDT), and the bird's location was flagged every minute. A time delay of 2 mins preceded sampling in each territory to reduce bias towards conspicuous sites, and we varied start times among territories. If the male was lost during the 30-min sampling period, each minute it was missing was recorded as a lost point. We worked in pairs which increased our ability to keep track of individuals and reduced bias towards flagging conspicuous sites. One person would walk directly under the bird to hang the flag while the other stood back keeping watch of the bird's location. This reduced bias towards flagging only singing locations, because the observer with a better view of the bird could direct their partner to stand below it. To reduce bias towards more conspicuous sites, we did not require that the bird be in view to hang a flag, for instance an observer could flag a perch from where a bird had recently flown, or where the bird could be heard singing directly above the observer. We set minimum criteria to include a sampling bout in final territory calculations if at least eight unique locations were flagged or if we observed an individual at least 15 mins of the 30-min period.

We set a minimum criterion of at least 50 observations to include a territory in territory size calculations and analyses.

Territory Delineation.—Well-defined territories were revisited in July–August of 2005 to obtain spatial coordinates for the territory flags. We used Trimble GeoExplorer CE series GPS units and corrected coordinates using GPS Pathfinder software. Accuracy of corrected GPS points was 0.6–9.0 m with most points accurate to at least 3 m and points on ridgetops accurate to 0.5–1.5 m.

Territory sizes were estimated using both minimum convex polygon (MCP) (Mohr 1947, Jones et al. 2001) and fixed kernel methods (Worton 1987, Barg et al. 2005). We used CALHOME software (Kie et al. 1994) for calculating MCPs and the Animal Movements extension (Hooge and Eichenlaub 2000) in ArcView 3.2 (Environmental Systems Research Institute 1999) to calculate fixed kernel density areas. We used the least-squares cross-validation method to determine the smoothing parameter. We selected the 50% kernel density isopleth to represent areas of high use (core areas) within the territory and the 95% isopleth for the territory as they have been commonly applied in previous studies (Worton 1989, Frank and Lutz 1999, Rivera et al. 2003).

Measurement of Gaps.—We defined a canopy gap as a break in the canopy at least 5 m in diameter (Pickett and White 1985) across the broadest width and a distance of at least 7 m down from the surrounding canopy to the next vegetative strata. The diameter of each gap was measured in the field with a range finder and receiving panel and the vertical difference in vegetation was assessed as greater or less than 7 m by field technicians that were well-practiced in estimating vegetation heights. All canopy gaps that were included within, intersected, or were located along the edge of a cerulean territory (within 5 m) were mapped in the field. Each gap was assigned a type indicating whether it was associated with a trail or gasline, treefall, grapevine, or food plot.

Canopy gaps were mapped in the field using a combination of GPS coordinates to delineate the edges of the gap, measurements of gap dimensions, field sketches of each gap, and compass bearings of gap edges (Perkins 2006). We visually estimated and placed into categories canopy height surrounding each gap (>12–18 m, >18–24 m, and >24 m) and the vegetation height within it (0–3 m, >3–6 m, >6–12 m, >12–18 m). Additionally, we quantified gap availability at each of the two sites in stratified random plots that were circular and equal in size to the estimated mean territory MCP of bird territories mapped on the sites in 2004. Locations for random plots were generated in Hawth's tools (Beyer 2004) and were equal in number to the number of territories mapped on each ridge. Random plots were stratified by overlaying a grid over each study area and allowing one plot per grid square. Random plots were truly random and did overlap with territories in some instances.

We calculated canopy gap density within territories and random plots as the number of gaps that intersected or occurred within the territory boundary, standardized to the number of gaps/500 m^2. We estimated gap proportion as the percent area of each territory (or random plot) that contained gaps (i.e., lacked canopy cover). Gap size was the mean size of all gaps that intersected or occurred within the territory boundary. Linear gaps, such as roads and powerlines that lacked a discrete area, were excluded from gap size calculations.

Gaps were assigned a location relative to the territory; each was designated as a 'periphery' or 'territory' gap. Gaps with <25% of their area located within the territory, or gaps that occurred outside the territory but within 5 m of the territory boundary, were classed as 'periphery' gaps. We used the 5-m criterion to account for GPS accuracy and thus included some gaps that were located on the very edge of territories. Gaps were considered a 'territory' gap if ≥25% of the gap occurred within the territory boundary.

Statistical Analyses.—We used R version 2.15 (R Development Core Team 2012) for all analyses. Statistical significance was set at $\alpha = 0.05$. We tested data for normal distribution prior to analysis. We square root transformed gap proportion and territory size and log transformed gap density to approximate a normal distribution prior to analyses. We used transformed variables in statistical tests but report untransformed values in tables and text.

We compared 2005 territory (95% kernel) and core area (50% kernel) size between the two study sites (HR and SR) with Student's two-tailed *t*-tests for unequal variances. We also tested whether the sizes of gaps intersecting territories differed between HR and SR with Student's two-tailed

t-tests for unequal variances. We used analysis of variance, with site as a random blocking factor, to determine whether gap density or proportion differed among core areas, territories, and random plots. We used Waller-Duncan *K*-ratio *t*-test to identify which means differed from each other. This test compares Type I and Type II error rates based on Bayesian principles (Steel and Torrie 1980). We set $K = 100$ which roughly corresponds to an α-value of 0.05 (Waller and Duncan 1969, Steel and Torrie 1980).

We used Pearson's chi-square test of independence to determine if gap characteristics (size, vegetation height, and canopy height) differed between territories, core areas, and random plots. Categories were combined when necessary to meet the assumptions of minimum expected cell counts. To investigate whether ceruleans were selecting certain sizes of gaps occurring within territories, we categorized gap size into 4 classes based on the distribution of the data (<50 m^2, 50–100 m^2, 100–300 m^2, or >300 m^2). Data were not pooled across the two sites for tests comparing vegetation heights within gaps and surrounding canopy heights to availability, because these parameters differed between the two sites and resulted in different outcomes of the test. We used Pearson's chi-square test of independence to determine if gap sizes differed between territory and periphery gaps and Fisher's Exact Test to determine the same for gap type. To determine which categories contributed the most to the outcome of each significant chi-square test, we calculated standardized residuals for each cell in the chi-square table with the equation ([observed-expected]/$\sqrt{\text{expected}}$) (Haberman 1973, Reynolds 1977, Newman and Waters 1984). The highest absolute values represent the greatest differences in observed and expected values contributing to the outcome of the test. Residuals with an absolute value greater than or equal to the tabled critical two-tailed 0.05 value $z_{.05} = 1.96$ indicate cells where there was a significant difference between observed and expected values (Sheskin 2004).

RESULTS

Twenty-five territories were delineated and of these, four were omitted from analyses because they did not meet the minimum criterion of 50 observations. The remaining 21 territories had a mean of 86 (range = 64–117) locations per territory.

TABLE 1. Number of territories of Cerulean Warblers (n) and mean size (± SE and range, m^2) in Wetzel County, WV estimated by minimum convex polygon (MCP), 95% fixed kernel, and 50% fixed kernel core area methods for two ridges in May–June 2005.

		n	Mean ± SE	Range
Territory				
	MCP	21	3689 ± 665	546–13203
	95% Kernel			
	Combined	21	3409 ± 558	603–9617
	Hart Ridge	14	3016 ± 645	603–8909
	Snake Ridge	7	4193 ± 1073	645–9616
Core area				
	50% Kernel			
	Combined	21	457 ± 88	43–1661
	Hart Ridge	14	345 ± 69	43–1009
	Snake Ridge	7	680 ± 209	45–1661

Territory Size.—Mean MCP territory size was 3,689 m^2 (Table 1) and the 95% kernel density estimate of 3,408 m^2 was only slightly smaller than the mean MCP estimate. The 95% kernel ($t_{10} = -0.9$, $P = 0.37$) and the 50% kernel ($t_7 = -1.5$, $P = 0.17$) estimates did not differ between the two study sites.

Gap Density and Proportion.—Gap densities were greater within core areas than in territories or random plots ($F_{2,63} = 9.56$, $P = <0.0001$, Table 2). Gap densities in territories differed between sites ($F_{1,63} = 9.54$, $P = 0.003$); they were greater on HR (1.0 gaps/500 m^2, range: 0.5–1.8) than on SR (0.7 gap/500 m^2, range: 0.4–1.2).

We found no differences in gap proportion among territories, core areas, and random plots ($F_{2,63} = 2.58$, $P = 0.08$, Table 2) or between sites ($F_{1,63} = 1.23$, $P = 0.27$). The mean gap proportion of territories on HR was 17% (range: 3–38%) and 13% (range: 9–17%) on SR.

Gap Size.—Size of gaps that intersected territories ranged from 12–3,163 m^2 although most gaps (86%) were <500 m^2 (Fig. 1). Gap size did not differ between core areas, territories, and random plots ($\chi^2_6 = 5.85$, $P = 0.44$, Fig. 1). The sizes of gaps intersecting territories also did not differ between the two study sites ($t_{95} = 1.0$, $P = 0.31$).

Gap size differed between gaps located on territory peripheries and within territories ($\chi^2_3 = 9.56$, $P = 0.022$, Fig. 2). Small gaps in the 50–100 m^2 category occurred more frequently within territories and less frequently on the periphery. The largest size class of gaps, >300 m^2, occurred

TABLE 2. Canopy gap measurements within Cerulean Warblers' territories, core areas, and random plots in Wetzel County, WV in 2005.

Variable	Site	Territory Mean ± SE	Random Mean ± SE	Core Mean ± SE
Gap density (#/500 m^2)[a]				
	HR[c]	1.0 ± 0.1	0.9 ± 0.1	2.9 ± 0.5
	SR[d]	0.7 ± 0.1	0.8 ± 0.1	1.1 ± 0.3
Gap proportion (%)[b]				
	HR	17 ± 3	22 ± 3	17 ± 5
	SR	13 ± 1	17 ± 2	12 ± 4
Average gap size (m^2)[a]				
	HR	306.0 ± 61.2	331.5 ± 71.2	324.6 ± 149.6
	SR	235.4 ± 33.7	175.3 ± 30.6	216.9 ± 38.2

[a] Included any gap that intersected the territory.
[b] Included only the amount of gap area that fell within the territory.
[c] Hart Ridge (HR).
[d] Snake Ridge (SR).

more frequently than expected on peripheries and less frequently than expected within territories.

Gap Type.—The most common type of gap that intersected cerulean territories was autogenic treefall gaps which comprised 68% of gaps. Gap types did not differ among territories, core areas, and random plots ($\chi^2_3 = 3.17$, $P = 0.37$) but did differ between territory peripheries and within territories (Fishers exact, df = 3, $P = <0.001$, Fig. 3). The greatest difference between observed and expected values was the location of food plots, which occurred only on territory peripheries. Trail gaps were also more frequently on territory peripheries. Treefall gaps were found more often than expected within territories and less than expected on the peripheries of territories.

Vegetative Structure of Gaps.—Vegetation height within the gaps did not differ between territories and random plots on SR ($\chi^2_2 = 1.04$, $P = 0.60$; Fig. 4). The sample size there was not large enough to test core areas because it resulted in expected cell values that were <5. While vegetation heights did not statistically differ among territories, core areas, and random plots on HR ($\chi^2 = 9.34_4$, $P = 0.05$), gap vegetation heights in the >12 m category on HR occurred more frequently within core areas than in

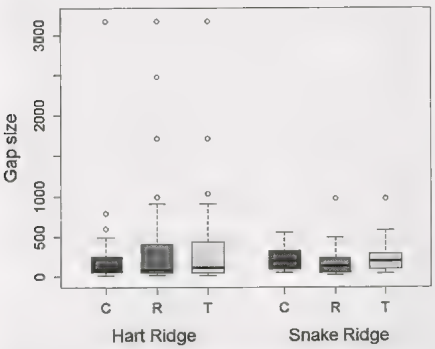


FIG. 1. Boxplot displaying the range, median, first quartile and third quartile of canopy gaps sizes (m^2) that intersected Cerulean Warblers' core areas (C), territories (T), and random plots (R), on two study sites.

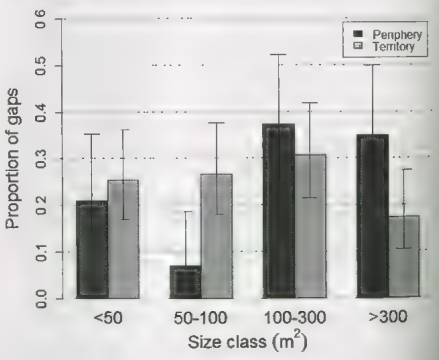


FIG. 2. Proportion of canopy gaps located within Cerulean Warblers' territories or on territory peripheries by size class (m^2) in 2005 ($\chi^2_3 = 9.56$, $P = 0.022$). Error bars represent the 95% confidence interval.

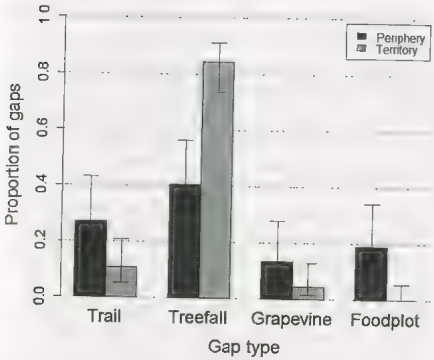


FIG. 3. Proportion of gaps located within Cerulean Warblers' territories or on territory peripheries by type (Fishers exact, df = 3, P = <0.001). Error bars represent the 95% confidence interval.

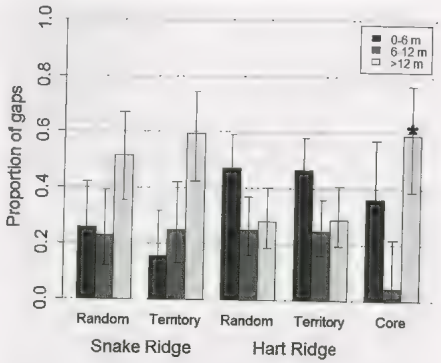


FIG. 4. Vegetation heights within canopy gaps located in Cerulean Warblers' territories, territory core areas, and random plots (SR: $\chi^2_2 = 1.04$, $P = 0.60$, HR $\chi^2_4 = 9.34$, $P = 0.05$). Core area on SR was not tested, because the small sample size resulted in expected cell values <5. Stars indicate categories where chi-square residuals had an absolute value greater than or equal to the tabled critical two-tailed 0.05 value $z_{.05} = 1.96$. Error bars represent the 95% confidence interval.

territories and random plots (Fig. 4), and these results may still be biologically meaningful.

Canopy heights surrounding gaps did not differ among random plots, territories, and core areas on HR ($\chi^2_2 = 2.21$, $P = 0.33$) but did differ on SR ($\chi^2_2 = 12.54$, $P = 0.002$). On SR, gaps with surrounding canopy heights of >24 m occurred more frequently than expected within territories and core areas compared with availability, while random plots had significantly more gaps with surrounding canopy heights of <24 m (Fig. 5).

DISCUSSION

Gap Type and Size.—We documented a variety of gap types and sizes incorporated within male territories. Although the majority of gaps were treefall gaps, we found no indication that birds selected particular types of gaps. However, some gap types, such as trails and foodplots, were more likely to occur on the periphery of territories, while treefall gaps were more often located within them. Treefall gaps may be similar in structure to gaps present in old-growth forest with which this species was historically associated (Hamel 2000, Hunter et al. 2001) and perhaps there is selection for trail gaps on territory boundaries. We often observed cerulean males using the opening in the canopy above a ridgeline trail as a territory boundary when counter-singing and this could be a key location for song projection and high visibility to other males. Similarly, Weakland and Wood (2005) reported that ceruleans did not avoid internal edges (i.e., smaller edges such as partially open canopy roads and trails within forested locations) as territories occurred more frequently than expected (63%) near roads with patchy overhead canopy cover. However, since use is less on the edges of a kernel density distribution, it could also be that gaps associated with trails and foodplots, though not avoided, were just used less

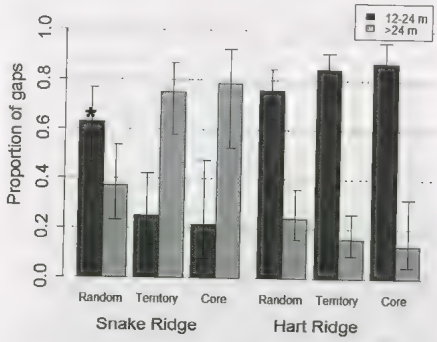


FIG. 5. Canopy heights surrounding canopy gaps located in Cerulean Warblers' territories, territory core areas, and random plots (SR: $\chi^2_2 = 12.54$, $P = 0.002$, HR: $\chi^2_2 = 2.21$, $P = 0.33$). Stars indicate categories where chi-square residuals had an absolute value greater than or equal to the tabled critical two-tailed 0.05 value $z_{.05} = 1.96$. Error bars represent the 95% confidence interval.

often within the territory than treefall gaps. The use of gaps that intersected territories could also relate to gap size as treefall gaps were generally small and food plots were some of the largest gaps on our study site and were likely not included within territory boundaries for this reason.

We did not detect a difference in frequency of gaps by size class in territories or core areas compared with random plots. However, the largest gaps (>300 m^2) occurred more often than expected on territory peripheries, while smaller gaps (<100 m^2) were more often included within territories. Ceruleans may include smaller gaps within territories and may place territories near larger gaps, but do not incorporate large portions of them within the defended boundary. Ceruleans are known to avoid large-scale edge such as mountaintop removal mines (Bosworth 2003, Weakland and Wood 2005, Wood et al. 2006). It may be that even the largest sizes of gaps (300–3,163 m^2) present on the sites we surveyed during the time of our study were not large enough that they would be avoided. Buehler et al. (2013) suggested that Cerulean Warblers avoid large clearings because of declines in nesting success resulting from predation and parasitism, instead of responding to the presence of the edge or clearing itself. However, the response of ceruleans to the creation of larger gaps remains unclear and may vary by site. Boves et al. (2013a), in a robust study spanning multiple states, found that intermediate and heavy forest canopy reductions (on 10-ha plots) greatly increased densities of ceruleans but nesting success declined significantly, depending on the region. Bakermans and Rodewald (2009) found that adjacent clearcuts (5.7–15.6 ha in size) did not reduce density or nesting success of ceruleans and Wood et al. (2005) found ceruleans were tolerant of clearcuts and two-age harvests adjacent to mature forest stands. Perhaps the gaps occurring on territory peripheries in our study area were also not large enough to cause increases in predation and parasitism, in a heavily forested landscape, and so were not avoided.

Gap Density and Proportion.—Core areas of territories had greater gap densities than territories or available habitat. Thus, cerulean males appear to focus their activities in more ''gappy'' portions of their territory. Similarly, Boves et al. (2013b) found ceruleans inhabiting highly forested landscapes, such as our study area, selected microhabitat that was open-canopy.

The question remains why ceruleans may be attracted to gaps in the forest canopy. Increased song projection has been cited as one benefit of canopy gaps to forest songbirds. Barg et al. (2006) suggested that cerulean males may spend more time near canopy gaps because the openings enhance song by limiting reverberation and attenuation, and the gaps also enable territorial males to be more conspicuous. Gaps may provide foraging opportunities, as well, since more light results in increased foliage surrounding the gap and increased prey abundance (Noss 1991, Rotenberry et al. 1995, Smith and Dallman 1996). However, core areas, which we found to have high gap densities, do not appear to be foraging hotspots (Barg et al. 2006, Perkins 2006, Wood and Perkins 2012). Barg et al. (2006) found a higher density of song posts within core areas of territories which suggests that they are used primarily for singing. Wood and Perkins (2012) found that singing occurred more frequently than expected in territory core areas when compared with foraging. Nonetheless, if insect abundance is higher in or near gaps, it is possible that males forage opportunistically at a greater success rate while singing, than they would otherwise in a dense canopy.

We expected the proportion of core areas covered by gaps to be significantly more than territories or random plots, given the selection for higher gap densities within them, but this was not the case. Thus ceruleans in this study favored a canopy structure that had abundant small gaps but retained canopy cover similar to the surrounding forest. There is potentially a threshold where the loss of foliage associated with increasing gap area leads to declines in habitat quality, such as lower prey availability or reduced nest success from predation. Therefore the costs of placing a territory in a location with reduced canopy cover, may outweigh the benefits gained from the resources that canopy gaps provide. Previous research has found reduced nest success for Cerulean Warblers after reductions in forest canopy in some regions (Jones et al. 2001, Boves et al. 2013a).

Vegetative Structure of Gaps.—Our findings on SR, that ceruleans selected gaps with surrounding canopy cover >24 m, is likely related to the species affinity for a dense upper canopy and large tall trees (Lynch 1981, Jones and Robertson 2001). Perhaps the canopy gaps, with tall trees surrounding them, served as ideal singing locations to

enhance song projection (Barg et al. 2006, Wood and Perkins 2012). Our findings are similar to previous studies which have also found an association between cerulean presence and a tall upper canopy stratum. Weakland and Wood (2005) and Bosworth (2003) found ceruleans were positively related to foliage cover at >24 m. Carpenter et al. (2011) found an association of ceruleans with taller canopies and Jones and Robertson (2001) found greater nest success among sites with foliage cover >18 m.

In addition to presence of a tall canopy, previous research has demonstrated the importance of understory and lower canopy cover. Weakland and Wood (2005) found territory densities were positively related to foliage cover at 6–12 m. Bakermans and Rodewald (2009) found that cerulean densities and nesting success were positively related to high understory stem density. Jones and Robertson (2001) found greater nest success among sites with greater foliage cover at 6–12 m and in one year, cover >18 m. We found that ceruleans on HR selected vegetation heights of >12 m within gaps. Perhaps the increased cover provided protection from predators below or increased foraging opportunities. Previous research has documented the use of forest understory and lower- and mid-canopy strata for foraging. Bakermans and Rodewald (2009) noted that female ceruleans frequently drop into the understory during foraging bouts and Wood and Perkins (2012) found that lower- and mid-canopy strata were used more often for foraging, perching, and preening. More research is needed to determine the importance of mid-canopy vegetative stratum, especially in gaps located in territory or core areas, to determine if this vegetative structure is important range-wide or if it is site-specific. Despite the unknown utility provided by the vegetative structure within and surrounding gaps, our finding that selection is occurring and differs among sites may demonstrate adaptability or differing needs depending on forest structure.

Management/Conservation Implications.—Bakermans and Rodewald (2009) suggested that the creation of canopy gaps >40 m^2 in size might benefit management for Cerulean Warblers. While there is overlap in the sizes of gaps selected between their study and ours, we found selection for canopy gaps 50–100 m^2 in size within territories, and that had advanced vegetative growth >12 m within them or surrounded by >24 m canopy. Thus, forestry practices such as light group-selection harvests that create openings ~50–100 m^2 are likely compatible with management for this species. Harvests conducted in dense second-growth stands with a uniform canopy, that expose crowns of trees to increased light and allow already established regeneration to grow into a stratified canopy, may create a canopy structure favored by this species.

ACKNOWLEDGMENTS

Funding was provided by the Wildlife Diversity Program within the Wildlife Resources Section of the West Virginia Division of Natural Resources (WVDNR). Logistic and administrative support was provided by the USGS WV Cooperative Fish and Wildlife Resources Unit and the Division of Forestry and Natural Resources at West Virginia University. Land access was provided by WVDNR. Dr. J. W. Edwards, S. P. Olcott, Dr. S. Stoleson, and two anonymous reviewers provided comments on earlier versions of this paper. M. Carder, J. L. Eells, M. R. Lutmerding, L. M. McKenzie, B. L. Miller, J. L. Saville, and A. Stripple, provided field assistance. Additional support was provided by J. M. Strager (GIS), Dr. G. E. Seidel (statistics), Dr. T. G. Howard (statistics), B. Nolan (field site logistics), and R. Nestor (administrative). This study was performed under the auspices of West Virginia University ACUC protocol #04-0302. Use of tradenames does not imply endorsement by the Federal government.

LITERATURE CITED

Bakermans, M. H. and A. D. Rodewald. 2009. Think globally, manage locally: the importance of steady-state forest features for a declining songbird. Forest Ecology and Management 258:224–232.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Barg, J. J., D. M. Aiama, J. Jones, and R. J. Robertson. 2006. Within-territory habitat use and microhabitat selection by male Cerulean Warblers (*Dendroica cerulea*). Auk 123:795–806.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. www.spatialecology.com/htools (accessed 15 Sep 2005).

Blake, J. G. and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103:328–340.

Bosworth, S. B. 2003. Cerulean Warbler relative abundance and frequency of occurrence relative to large-scale edge. Thesis, West Virginia University, Morgantown, USA.

Boves, T. J., D. A. Buehler, J. Sheehan, P. B. Wood, A. D. Rodewald, J. L. Larkin, P. D. Keyser, F. L. Newell, G. A. George, M. H. Bakermans, A. Evans, T. A. Beachy, M. E. McDermott, K. A.

PERKINS, M. WHITE, AND T. B. WIGLEY. 2013a. Emulating natural disturbances for declining late-successional species: a case study of the consequences for Cerulean Warblers (*Setophaga cerulea*). PLoS ONE e52107.

BOVES T. J., D. A. BUEHLER, J. SHEEHAN, P. B. WOOD, A. D. RODEWALD, J. L. LARKIN, P. D. KEYSER, F. L. NEWELL, A. EVANS, G. A. GEORGE, AND T. B. WIGLEY. 2013b. Spatial variation in breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) throughout the Appalachian Mountains. Auk 130:46–59.

BUEHLER, D. A., P. B. HAMEL, AND T. BOVES. 2013. Cerulean Warbler (*Setophaga cerulea*), The birds of North America. Number 511.

CARPENTER, J. P., .Y. WANG, C. SCHWEITZER, AND P. B. HAMEL. 2011. Avian community and microhabitat associations of Cerulean Warblers in Alabama. Wilson Journal of Ornithology 123:206–217.

ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 1999. ArcView GIS: release 3.2. Environmental Systems Research Institute, 1992–1999, Redlands, California, USA.

FRANK, R. A. AND R. S. LUTZ. 1999. Productivity and survival of Great Horned Owls exposed to dieldrin. Condor 101:331–339.

GORHAM, L. E., S. L. KING, B. D. KEELAND, AND S. MOPPER. 2002. Effects of canopy gaps and flooding on homopterans in a bottomland hardwood forest. Wetlands 22:541–549.

HABERMAN, S. J. 1973. The analysis of residuals in cross-classified tables. Biometrics 29:205:220.

HAMEL, P. B. 2000. Cerulean Warbler status assessment. United States Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

HAMEL, P. B., D. K. DAWSON, AND P. D. KEYSER. 2004. How we can learn more about the Cerulean Warbler (*Dendroica cerulea*). Auk 121:7–14.

HOOGE, P. N. AND B. EICHENLAUB. 2000. Animal movement extension to ArcView. Version 2.0. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, Alaska, USA.

HUNTER, W. C., D. A. BUEHLER, R. A. CANTERBURY, J. L. CONFER, AND P. B. HAMEL. 2001. Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29:440–455.

JONES, J., R. D. DEBYUYN, J. J. BARG, AND R. J. ROBERTSON. 2001. Assessing the effects of natural disturbance on a Neotropical migrant songbird. Ecology 82:2628–2635.

JONES, J. AND R. J. ROBERTSON. 2001. Territory and nest-site selection of Cerulean Warblers in eastern Ontario. Auk 118:727–735.

KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1994. Calhome: a home range analysis program, Version 1. nhsbig.inhs.uiuc.edu/wes/home_range.html (accessed 15 Sep 2004).

LYNCH, J. M. 1981. Status of the Cerulean Warbler in the Roanoke River basin of North Carolina. Chat 45:29–35.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

MORSE, D. H. 1976. Variables affecting the density and territory size of breeding spruce wood warblers. Ecology 57:290–301.

NEWMAN, R. M. AND T. F. WATERS. 1984. Size-selective predation on *Gammarus pseudolimnaeus* by trout and sculpins. Ecology 65:1535–1545.

NOSS, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old growth Florida hammock. Natural Areas Journal 11:34–47.

OLIARNYK, C. J. AND R. J. ROBERTSON. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. Wilson Bulletin 108:673–684.

PERKINS, K. A. 2006. Cerulean Warbler selection of forest canopy gaps. Thesis, West Virginia University, Morgantown, USA.

PICKETT, S. T. A. AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, USA.

R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

REYNOLDS, H. T. 1977. The analysis of cross-classifications. Free Press, New York, New York, USA.

RIVERA, J. H. V., W. J. MCSHEA, AND J. H. RAPPOLE. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. Auk 120:632–644.

ROTENBERRY, J. T., R. J. COOPER, J. M. WUNDERLE, AND K. G. SMITH. 1995. When and how are populations limited? The roles on insect outbreaks, fire, and other natural perturbations. Pages 55–84 *in* Ecology and management of migratory birds: a synthesis and review of critical issues (T. E. Martin and D. M. Finch, Editors). Oxford University Press, Oxford, England.

ROTH, K. L. AND K. ISLAM. 2008. Habitat selection and reproductive success of Cerulean Warblers in Indiana. Wilson Journal of Ornithology 120:105–110.

SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI, JR., AND W. A. LINK. 2011. The North American Breeding Bird Survey, results and analysis 1966–2010. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

SHESKIN, D. J. 2004. Handbook of parametric and non parametric statistical procedures. CRC Press LLC, Boca Raton, Florida, USA.

SMITH, R. AND M. DALLMAN. 1996. Forest gap use by breeding Black-throated Green Warblers. Wilson Bulletin 108:588–591.

STEEL, R. G. D. AND J. H. TORRIE. 1980. Principles and procedures of statistics, a biometrical Approach. Second Edition. McGraw-Hill, New York, USA.

WALLER, R. A. AND D. B. DUNCAN. 1969. A Bayes rule for the symmetric multiple comparisons problems. Journal of the American Statistical Association 64:1484–1503.

WEAKLAND, C. A. AND P. B. WOOD. 2005. Cerulean Warbler (*Dendroica cerulea*) microhabitat and landscape-level habitat characteristics in southern West Virginia. Auk 122:497–508.

WOOD, P. B., S. B. BOSWORTH, AND R. DETTMERS. 2006. Cerulean Warbler abundance and occurrence relative to large-scale edge and habitat characteristics. Condor 108:154–165.

WOOD, P. B., J. P. DUGUAY, AND J. V. NICHOLS. 2005. Cerulean Warbler use of regenerated clearcut and two-age harvests. Wildlife Society Bulletin 33:851–858.

WOOD, P. B. AND K. A. PERKINS. 2012. Behavioral activities of male Cerulean Warblers in relation to habitat characteristics. Wilson Journal of Ornithology 124:497–505.

WORTON, B. J. 1987. A review of the models of home range for animal movement. Ecological Modeling 38:277–298.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

The Wilson Journal of Ornithology 126(2):298–304, 2014

HABITAT REQUIREMENTS OF THE ENDANGERED AMAMI THRUSH (*ZOOTHERA DAUMA MAJOR*), ENDEMIC TO AMAMI-OSHIMA ISLAND, SOUTHWESTERN JAPAN

TAKU MIZUTA[1]

ABSTRACT.—Amami Thrushes (*Zoothera dauma major*) are endemic birds distributed on Amami-Oshima Island in southwestern Japan. The population is considered to have declined during the latter half of the 20th century, mainly because of deforestation. I investigated the breeding habitat of Amami Thrushes in order to contribute to conservation efforts for these endangered birds. Field surveys showed that the thrushes prefer old-growth broad-leaved forests for breeding habitat. Both male and female parents cared for the nestlings, and most food items delivered for nestlings were earthworms, which were more abundant on the forest floor in older forests than in younger forests. Nests were placed on forks of large tree branches, rock ledges, and epiphytic ferns in middle to low strata of the forest. Older forests contained more large trees than younger forests, and epiphytic ferns were distributed in old-growth forests. The thrushs' preference for old-growth forests as breeding habitat was explained by the abundance of food and nesting resources in that environment. These results suggest that the preservation of old-growth broad-leaved forests should be given top priority if Amami Thrushes are to be protected. *Received 24 June 2013. Accepted 24 December 2013.*

Key words: Amami Thrush, Amami-Oshima Island, broad-leaved forest, earthworm, forest age, island-endemic species, Ryukyu Archipelago.

Island-endemic birds are particularly vulnerable to extinction (Newton 1998, Biber 2002). More than 90% (115 of 126 spp.) of extinct birds recorded since 1600 AD were island-dwelling species (Newton 1998). Among over 1,000 threatened bird species in the world in the late 20th century, 39% (402 spp.) were restricted to islands (Johnson and Stattersfield 1990). Today, island-birds in the Oceanic realm are understood to be substantially more threatened and to have declined faster, compared to the birds in other realms (BirdLife International 2013). Recent declines in island-bird populations have been caused primarily by human activities, particularly by habitat destruction (Johnson and Stattersfield 1990, Newton 1998) and introduction of mammalian predators (Blackburn et al. 2004, Karels et al. 2008). To make effective conservation plans for endangered, island-endemic species, it is necessary to examine the habitat requirements of the target species and to assess the impact of habitat destruction and introduced predators on the population. Since conditions of breeding habitat are an important factor affecting breeding success and population dynamics of birds, the study of natural history, including breeding ecology, is essential for the conservation of endangered species (e.g., Rodríguez and Moreno 2008, Becker et al. 2010).

Amami Thrushes (*Zoothera dauma major*) are birds endemic to Amami-Oshima Island in southwestern Japan; they are categorized as ''Vulnerable'' on the Japanese Red List compiled by the Ministry of the Environment (MOE) of the Japanese Government (MOE 2006). Several studies have been undertaken on the natural history of Amami Thrushes (see BirdLife International 2001); however, many of them were based on occasional observations that delivered limited information. To assess the species current status and accurately determine its vulnerability, it is crucial to investigate its natural history. Understanding the resources required for nesting and rearing offspring is particularly important for drawing up concrete conservation plans for protecting breeding habitat.

The Amami Wildlife Conservation Center has conducted field research on Amami Thrushes since the Protection/Propagation Program was established (MOE 1999). Apart from the program, some researchers conducted nest observations and recorded fragmentary information about the species' breeding behavior (Khan and Yamaguchi 2000, Takashi et al. 2002). The Amami Ornithologists' Club (AOC) also started a count survey for singing Amami Thrushes in 1998, which was supported by many volunteers (Khan and Takashi 2006, AOC 2008). In the present study, the natural history of Amami Thrushes, particularly the characteristics of breeding habitat and breeding

[1] Amami Wildlife Conservation Center, Koshinohata 551, Ongachi, Yamato, Oshima, Kagoshima 894–3104, Japan; e-mail: TAKU_MIZUTA@env.go.jp

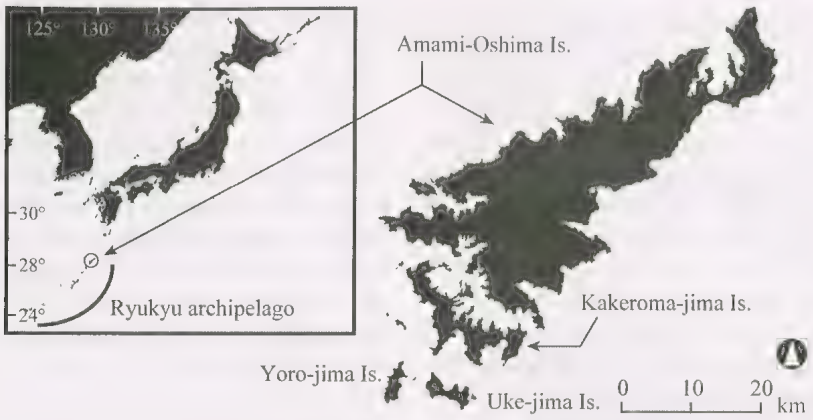


FIG. 1. Map of Amami-Oshima and its peripheral islands in the Ryukyu Archipelago, southwestern Japan.

ecology, is examined in order to contribute to further conservation of these endangered, island-endemic birds.

METHODS

Study Site and Species.—Amami-Oshima is the second largest island (712.39 km^2) in the Ryukyu Archipelago, a chain of islands in southwestern Japan (Fig. 1). Despite its small geographic area, the archipelago includes rich fauna and flora with high endemism (Biodiversity Center of Japan 2010). As an endemic bird, the Amami Thrush exists only on Amami-Oshima Island. Formerly considered a distinct species (Brazil 1991, Clement and Hathway 2000), it was listed as "Critically Endangered" on the International Union for Conservation of Nature (IUCN) Red List (BirdLife International 2000). However, the present treatment as a subspecies of *Z. dauma* (Collar 2004, The Ornithological Society of Japan 2012) offers no conservation status (IUCN 2012). Regardless of the status, the population that has been recorded is critically small; according to estimations, a few more than 58 birds lived on the island in 1996 (AOC 1997); by the early 2000s, the estimated numbers rose to just 50–100 breeding pairs (MOE 2002). Although Amami Thrushes are considered to have been scarce even in early and mid 20th century (e.g., Kobayashi 1930, Hachisuka and Udagawa 1953), the population is inferred to have diminished rapidly during the mid 1950s and early 1970s, because large-scale forestry (i.e., clear-cutting of large areas of mature forests) began in 1954 and peaked in 1972 on Amami-Oshima Island, which destroyed the habitat of many endemic animals (Sugimura 1988). Several researchers claimed that the population was also depressed by predation by the invasive small Indian mongoose (*Herpestes auropunctatus*) introduced to the island in 1979 (MOE 2002, AOC 2008). Song-count surveys in recent years, however, show a gradual population increase in Amami Thrushes, owing to forest recovery as a consequence of slowing deforestation and possibly to actions taken to eradicate the mongoose (AOC 2008).

Evaluation of Breeding Habitat.—The first nest of Amami Thrushes was found and observed in 1999 (Khan and Yamaguchi 2000). A total of 49 nests have been found by several researchers and forestry workers. Among them, 26 nests were not being used for breeding when they were found, and have not been used since. I am convinced that they belonged to Amami Thrushes, because other species of birds on the island never use such a large-sized nest (see Results for nest size). I measured the characteristics of their nests (i.e., nest height, nest diameter, and canopy height of the nest site) and examined the substratum and materials from each nest after the breeding season was over. The exact location of each nest was pinpointed by a GPS receiver (Garmin eTrex Legend HCx) and overlaid on geographic data using a Geographic Information System (GIS) to examine habitat characteristics such as vegetation type and forest age of the nest site. Vegetation was classified using four types: "broad-leaved forest," "secondary forest," "mixed forest" (secondary forest mixed with the Ryukyu pine, *Pinus luchuensis*), and "open area" (grassland and farmland). Based on occasional observations in the studies previously conducted, Amami Thrushes were thought to prefer mature, broad-leaved forest (BirdLife International 2001, MOE 2002). Based on

this information, I searched for nests in mature broad-leaved forest and found six of the 49 there. More nests were searched for without regard to vegetation type: the author found 26 nests by following a bird carrying food sighted while driving a road on the island; 17 nests were found by other researchers and forestry workers by chance during their work (e.g., trapping mongoose), which was conducted irrespective of forest type. Habitat characteristics of the nest sites (i.e., vegetation type and forest age) were compared with 100 randomly selected points on a map of Amami-Oshima Island to evaluate breeding habitat. Six nests searched for and found in mature broad-leaved forest (mentioned above) were excluded from the analyses to remove any bias associated with searching for nests in that specific habitat; therefore, data from 43 nest sites were used in this analysis. Since 26 out of 43 nests were found by pursuing a bird sighted from the road, habitat characteristics of the nest site may be affected by the presence of road (road effect or edge effect: Seiler 2001, Fahrig and Rytwinski 2009). To remove this effect, a 100-m buffer was generated on both sides of the road, and the 100 random points were selected within this area using GIS. Differences in vegetation types between the nest site and the random points were compared using Fisher's exact test, and the differences in forest age were compared using the Mann-Whitney *U*-test.

Nest Observations.—In the 23 nests that were being used for breeding when they were found, the breeding stage and clutch/brood size were checked by looking inside the nests or assumed by observation of the provisioning behavior of the parents. The presence of fledglings was confirmed by video camera recording (see below) or by observation of fledglings around the nest. Parental care behavior during the nestling stage was recorded by setting a video camera (SONY DCR-SR62 and HDR-XR520) about 20 m away from the nest and filming for ~ 6 hrs every other day on average. A total of 214.41 hrs of recordings were made at 11 nests. These nest observations were made in three different breeding seasons (2009–2012). Because the occupiers of the observed nests were not color-ringed, it is possible that the nests observed in different seasons were occupied by some of the same pairs. However, they were assumed to belong to different pairs, because the 11 nests were all more than 800 m apart from each other (the nearest two nests occupied by different pairs in the same breeding season were 640 m apart; TM, pers. obs.). The nest observations were therefore treated as independent data. Sex of the parent could not be determined because of sexually monomorphic traits. Individuals visiting a nest were discriminated based on careful inspection of feather coloration patterns. Food items delivered by parents and the frequency of food provisioning were recorded from video images. A Generalized Linear Mixed Model (GLMM) with Poisson error distribution and a log link function was applied to determine the factors affecting the food provisioning rate: the number of provisioning visits by both parents was treated as a response variable, and the brood size and the number of days after hatching as explanatory variables. Because earthworms were the main food for nestlings, and because earthworm density on the forest floor was correlated with forest age (see Results), the forest age around the nest site may affect provisioning frequency. The mean forest age within a 300-m radius of the nest (assumed home range size based on the distance of the nearest two nests owned by different pairs; see above) was calculated using GIS, and was included in the GLMM as another explanatory variable. Explanatory variables were treated as fixed effects, and nest ID and research year were assumed to be random effects. Observation duration in one day was included in the GLMM as an offset.

Breeding Performance in Relation to Forest Age.—Forest age is considered to be a possible factor affecting territory quality because of its correlation with the earthworm density (see Results), and therefore, breeding performance of Amami Thrushes may be different in relation to the age of the forest around nests. To evaluate the effect of forest age on breeding performance, the mean forest age within a radius of 300 m of the nest was compared among the nests with different clutch/brood sizes. Clutch size was confirmed at eight nests, and brood size at fledging was confirmed at nine nests. Nest fates (i.e., success or failure of fledging) were confirmed at 21 nests, and the effect of the mean forest age on the fledging success was also examined among these nests. A GLMM with a Poisson error with a log link function was used to analyze the effect of the mean forest age on the clutch/brood sizes, and a GLMM with a binomial error was used for the analysis of fledging success. The clutch/brood sizes and nest fates were set as response variables, and the mean age of the forest around each nest was treated as an explanatory variable. The research year was assumed to be the random effect.

Assessing Earthworm Abundance.—Abundance of earthworms, the main food for nestlings (see Results), was expected to be an important factor in determining habitat quality. Since Amami Thrushes are reported to prefer mature broad-leaved forests for habitat (BirdLife International 2001, MOE 2002), mature forests were predicted to contain a greater abundance of earthworms than did younger forests. To verify this prediction, earthworm density was examined during the period from 15 June to 1 July 2011. Seventeen research sites were selected in forests of different ages, and nine plots were laid out in each research site in a grid pattern. To minimize plot trampling by researchers, data were collected from plots separated by more than 5 m (as in Duriez et al. 2006). Each plot was a 50 cm × 50 cm quadrat with 10 cm depth. The earthworms in these plots (a total of 153 plots) were then counted. Species of earthworms were not identified in the present study, because most of the 80 earthworms sampled preliminarily were undescribed species in the family Megascolecidae, including at least eight distinct types (Y. Minamiya, pers. comm.). A GLMM with a Poisson error with a log link function was used to analyze the effect of forest age on the number of earthworms in each plot. The number of earthworms was set as a response variable and the forest age of each plot was treated as an explanatory variable. The research site was assumed to be the random effect.

Statistical and Geographical Analyses.—R version 2.13.2 (R Development Core Team 2011) was used for statistical analyses and the lmer function from the lme4 package was used for GLMM analyses. Likelihood ratio tests were applied in the GLMM analyses by comparing models with and without the fixed effect for significant testing of each explanatory variable. ArcGIS 10.1 (Esri Inc.) was used for geographical analyses. Vegetation maps were provided by the sixth and seventh Vegetation Surveys of the National Survey on the Natural Environment conducted by the MOE. Data on forest age were provided by Kagoshima Prefecture.

RESULTS

Characteristics of Nest and Breeding Habitat.—Among the 49 nests located, 33 nests were found on the forks of large tree branches. One nest was built on the trunk of a snapped tree. Eight nests were placed on rock ledges beside streams or roads. Another seven nests were placed on an epiphytic fern called bird's nest fern (*Asplenium nidus*), which grows on the branches of large trees. Nests were placed at 3.43 ± 2.33 m (mean ± SD, range: 0.4–11.5 m, $n = 49$) above the ground, and the canopy height at the nest site was 11.53 ± 2.92 m (4.5–20.0 m, $n = 49$). The nest was a broad bowl-shaped structure made of a large quantity of moss, with an outside diameter of 22.1 ± 2.2 cm ($n = 27$). Fine roots and rhizomorphs were laid on the bottom of the nest cup. In the nests built in mixed forest, pine needles rather than roots/rhizomorphs were laid inside.

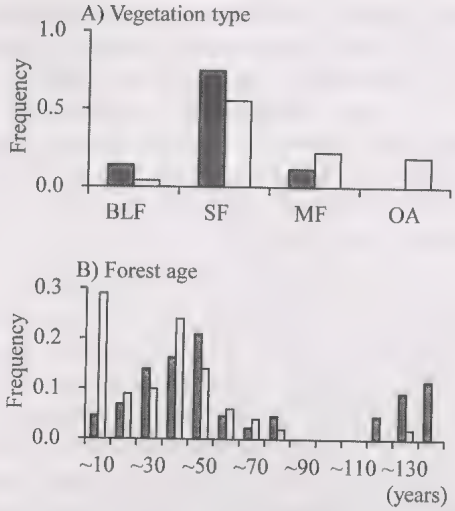


FIG. 2. Comparisons of frequency in A) vegetation type and B) forest age between 43 nest sites and 100 randomly selected points on Amami-Oshima Island. Filled bars indicate the nest site, and open bars indicate the random point. BLF: broad-leaved forest, SF: secondary forest, MF: mixed forest, and OA: open area.

Among the 43 nests located without searching in one particular vegetation type, six nests (14%) were found in broad-leaved forest, although the broad-leaved forest covers an area of 24.8 km^2, which is a mere 4% of the area of the island. Thirty-two nests were found in secondary forest, and five were found in mixed forest. On the other hand, among 100 randomly selected points, four points were placed in broad-leaved forest, 55 in secondary forest, 22 in mixed forest, and 19 in open areas. Vegetation types differed significantly between nest sites and random points (Fisher's exact test, $P < 0.001$; Fig. 2A). The forest age of nest sites was significantly higher than that of the random points (Mann-Whitney U-test, $Z = 4.17$, $P < 0.001$, Fig. 2B).

Information on Breeding and Parental Care Behavior at the Nest.—Among the 23 nests where

breeding was observed, 14 were in the incubation stage when they were found. Clutch size was three at four nests, two at four nests, and unknown at another six nests. Nine nests were found in the nestling stage. Brood size was three at three nests, two at three nests, one at one nest, and unknown at two nests. The presence of fledglings was confirmed at 10 nests. Eggs/nestlings disappeared before hatching/fledging at 10 nests. At one nest, nestlings were found dead in the nest after a heavy rainfall. The fate of another two nests could not be confirmed. The earliest and the latest fledglings during the breeding season were observed on 21 April 2009 and on 25 June 2012, respectively.

Predators of eggs/nestlings could not be identified, but nest observations provided some circumstantial evidence of nest predation. In 2007, Lidth's Jay (*Garrulus lidthi*), an endemic corvid species distributed on Amami-Oshima and two peripheral islands (Kakeroma-jima and Uke-jima; Fig. 1), came to a nest of Amami Thrushes and pecked nest materials a few days after egg disappearance. In 2010, a parent on a nest produced high-pitched alarm calls just after a Jungle Crow (*Corvus macrorhynchos*) called near the nest. Nestlings immediately crouched in the nest in response to the parent's alarm call.

The duration of the nestling stage (the number of days from hatching to fledging) could be confirmed at three nests, and lasted 15 days (two nests) and 16 days (one nest). Parental care was shared by two individuals at each of 11 observed nests. Brooding was done by one individual, and the other delivered food for nestlings. The former did not start food delivery until about 10 days after hatching, whereas the latter never took part in brooding. Time spent brooding by the former individual decreased as the nestlings got older. Food provisioning rate increased with brood size (likelihood ratio test, $\chi^2 = 11.04$, $P < 0.001$) and nestling stage ($\chi^2 = 39.60$, $P < 0.001$). Mean forest age within a radius of 300 m of the nest did not affect provisioning rate ($\chi^2 = 0.88$, $P = 0.35$).

A total of 581 feeding visits were recorded during 214.41 hrs of observation at 11 nests. Food items delivered on 453 visits (78%) were earthworms. Parents carried more than one earthworm (1–4) to the nestlings at once. Arthropods, including centipedes, millipedes, and Lepidoptera larvae, were delivered on 19 visits (3%). Food items were not identified on 109 visits (19%), because the parent's back or speed of movement obstructed the video view.

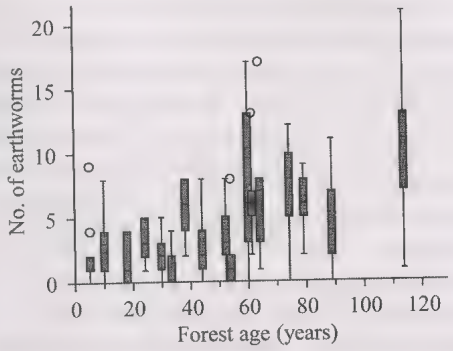


FIG. 3. Numbers of earthworms counted at 17 research sites of different forest ages. Each research site includes nine plots; earthworms were counted in a total of 153 plots. The boxes represent the interquartile range, and the horizontal lines inside the boxes are the median. The whiskers indicate up to 1.5 times the interquartile range. The circles above each whisker are outliers.

Breeding Performance in Relation to Forest Age.—Neither clutch nor brood size were significantly affected by mean forest age within a 300-m radius of the nest (likelihood ratio test, clutch size, $\chi^2 = 0.01$, $P = 0.91$; brood size, $\chi^2 = 0.04$, $P = 0.84$). Fledging success was also not affected by mean forest age ($\chi^2 = 0.75$, $P = 0.39$). Breeding performance of Amami Thrushes, therefore, did not differ regardless of the forest age around the nest.

Earthworm Abundance.—The number of earthworms on the forest floor varied among plots in each research site. The research site in the old-growth forest contained more earthworms than the site in the younger forest (likelihood ratio test, $\chi^2 = 15.59$, $P < 0.001$, Fig. 3).

DISCUSSION

Nests of Amami Thrushes were found abundantly in older broad-leaved forest (Fig. 2). Broad-leaved forest makes up only 4% of the island's area, but a total of 12 out of 49 nests (25%) were found in broad-leaved forest. Most food items delivered by the parents to the nestlings were earthworms, thus earthworms are likely a crucially important resource for breeding. It was confirmed that earthworms were distributed more abundantly in older forests than younger forests (Fig. 3). Old-growth broad-leaved forest is humid, and the forest floor tends to be wetter than that in younger forest (MOE 2002), creating an environment that may be more hospitable to earthworms. Amami Thrushes' preference for older forest in choosing breeding habitat is partly

explained by the abundance of earthworms in that environment. However, neither parental provisioning rate nor breeding performance (e.g., clutch size, brood size, and breeding success) were affected by the age of the forest around the nest in the present study. Relatively low territory quality in younger forest may be compensated for by the additional effort by parents to search for earthworm-abundant areas in the territory, because sometimes a considerable number of earthworms were found even in younger forests (Fig. 3). Further study with sufficient sample size is necessary to investigate the relationship between territory quality and breeding ecology as regards Amami Thrushes.

Nest structure and materials used by Amami Thrushes were similar to those of *Z. d. aurea* observed on the Main Island of Japan (Yamashina 1941, Kiyosu 1978). One peculiarity of the nesting habits of Amami Thrushes was the use of bird's nest fern as a substratum. This fern is distributed in tropical rain forests throughout the Old World, and is abundant in wet forested areas (Zhang et al. 2009). On Amami-Oshima Island, the bird's nest fern is distributed in relatively old-growth forest (TM, pers. obs.). Older forest also contains more large trees than younger forest. The forks of large tree branches are the important nesting substratum for Amami Thrushes. Therefore, suitable nesting substrata are more abundant in older forests than in younger forests, which may be another reason that Amami Thrushes prefer older forests.

Observation of 11 nests showed that one individual brooded and the other delivered food to nestlings. In *Z. d. aurea*, a female constantly stayed at the nest, while a male delivered food for the female and the nestlings (Cramp 1988). The brooding individual is likely to be the female and the feeding individual the male in the Amami Thrush as well, as suggested by Khan and Yamaguchi (2000). This observation indicates that the Amami Thrushes are socially monogamous.

Among the 23 nests at which breeding was observed, eggs/nestlings disappeared before hatching/fledging at 10 nests. The cause was not detected, but most of the disappearances were attributed to predation. Two corvid species, Lidth's Jay and the Jungle Crow, were suspected nest-predators (see Takashi et al. 2002). As these species are abundant throughout the island, they are expected to exert high predation pressure on nests of Amami Thrushes. Small Indian Mongooses may also be predators of the thrushes. However, Amami Thrushes have been relatively abundant in the area where mongoose density has been very high. On the other hand, only a few thrushes were recorded in the 1990s in the southern part of the island where the mongoose was not distributed (AOC 1997). Therefore, the impact of mongooses on the population of Amami Thrushes is not clear at present.

The present study confirmed the importance of old-growth forest for breeding Amami Thrushes, suggesting that forest of this type should be given top priority for preservation. The key habitat for the thrush is also coincident with that for Amami Woodcocks (*Scolopax mira*) and Amami rabbits (*Pentalagus furnessi*), two threatened endemic species that need equal consideration for conservation. The Japanese government is currently planning to designate a new national park area on Amami-Oshima Island, with the intent to list the Ryukyu Archipelago as a UNESCO World Natural Heritage Site in the near future (MOE 2012). This study is expected to serve as good reference material for the designation of the national park area, which is important for further conservation of these threatened species.

Subspecies are usually considered to be of lower conservation priority than species (Hazevoet 1996). Lack of phylogenetic study among *Z. dauma* subspecies in Eastern Asia has confused the conservation status of Amami Thrushes in the last dozen years (BirdLife International 2000, IUCN 2012; see Methods). It is necessary to confirm the phylogeny of *Z. dauma* subspecies, although conservation action is required regardless of taxonomic status.

ACKNOWLEDGMENTS

This study was conducted under the Protection/Propagation Program (PPP) for the Amami Thrush formulated by the MOE. I am grateful to the Rangers of the Amami Wildlife Conservation Center, S. Abe, T. Ishikawa, J. Tanaka and M. Tatara, for their management of the research, and to Y. Ito, Y. Kochi, T. Matsuda, Y. Nagai, T. Sakoda, and T. Watanabe for their field assistance. I also thank the members of the Amami Mongoose Busters, Amami Ornithologists' Club, Office of the Forestry Agency, and several researchers for providing information about nesting Amami Thrushes. I am indebted to Y. Minamiya for examination of earthworm species. Early manuscript drafts were kindly checked by B. McKay and T. Suzuki. Special thanks are due to members of the PPP Committee S. Hattori, K. Ishida, N. Ishii, H. Sakamoto, F. Yamada, and M. Yokota for their useful comments on the research.

LITERATURE CITED

AMAMI ORNITHOLOGISTS' CLUB (AOC). 1997. A population estimate of the endangered Amami Thrush made by counting singing birds. Strix 15:117–121 (in Japanese.)

AMAMI ORNITHOLOGISTS' CLUB (AOC). 2008. Breeding population changes of *Zoothera (dauma) major* based on singing bird counts (1999–2007). Strix 26:97–104 (in Japanese).

BECKER, C. D., H. L. MOUNCE, T. A. RASSMUSSEN, A. RAUCH-SASSEEN, K. J. SWINNERTON, AND D. L. LEONARD. 2010. Nest success and parental investment in the critically endangered Maui Parrotbill *Pseudonestor xanthophrys* with implications for recovery. Endangered Species Research 11:189–194.

BIBER, E. 2002. Patterns of endemic extinctions among island bird species. Ecography 25:661–676.

BIODIVERSITY CENTER OF JAPAN. 2010. Biodiversity of Japan: a harmonious coexistence between nature and humankind. Heibonsha, Tokyo, Japan.

BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Lynx Edicions and BirdLife International, Barcelona and Cambridge, UK.

BIRDLIFE INTERNATIONAL. 2001. Threatened birds of Asia: the BirdLife International red data book. BirdLife International, Cambridge, UK.

BIRDLIFE INTERNATIONAL. 2013. Birds in some regions, notably Oceania and Asia, have deteriorated in status faster than others. Presented as part of the BirdLife state of the world's birds. www.birdlife.org/datazone/sowb/casestudy/121 (accessed 31 Oct 2013).

BLACKBURN, T. M., P. C. CASSEY, R. P. DUNCAN, K. L. EVANS, AND K. J. GASTON. 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958.

BRAZIL, M. A. 1991. The birds of Japan. Christopher Helm, London, UK.

CLEMENT, P. AND R. HATHWAY. 2000. Thrushes. Christopher Helm, London, UK.

COLLAR, N. J. 2004. Species limits in some Indonesian thrushes. Forktail 20:71–87.

CRAMP, S. 1988. The birds of the Western Palearctic. Volume V. Oxford University Press, Oxford, UK.

DURIEZ, O, Y. FERRAND, AND F. BINET. 2006. An adapted method for sampling earthworms at night in wildlife studies. Journal of Wildlife Management 70:852–858.

FAHRIG, L. AND T. RYTWINSKI. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:21.

HACHISUKA, M. AND T. UDAGAWA.1953. Contribution to the ornithology of the Ryukyu Islands. Quarterly Journal of the Taiwan Museum 6:141–279.

HAZEVOET, C. J. 1996. Conservation and species lists: taxonomic neglect promotes the extinction of endemic birds, as exemplified by taxa from eastern Atlantic islands. Bird Conservation International 6:181–196.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN). 2012. IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org/search (accessed 22 Jan 2013).

JOHNSON, T. H. AND A. J. STATTERSFIELD. 1990. A global review of island endemic birds. Ibis 132:167–180.

KARELS, T. J., F. S. DOBSON, H. S.TREVINO, AND A. L. SKIBIEL. 2008. The biogeography of avian extinctions on oceanic islands. Journal of Biogeography 35:1106–1111.

KHAN, A. A. AND M. TAKASHI. 2006. Notes on Amami Thrush, *Zoothera (dauma) major* on Amami Oshima, Ryukyu Islands, Japan. Forktail 22:117–119.

KHAN, A. A. AND Y. YAMAGUCHI. 2000. First nidification and breeding biology of Amami Thrush *Zoothera dauma major* (Ogawa), Amami Oshima, Japan. Japanese Journal of Ornithology 49:139–144.

KIYOSU, Y. 1978. Nihon Chourui Daizukan I. Kodansha, Tokyo, Japan (in Japanese).

KOBAYASHI, K. 1930. On a collection of bird-skins and eggs from the Riu Kiu Islands. Tori 6:341–382 (in Japanese).

MINISTRY OF THE ENVIRONMENT (MOE). 1999. A plan for the Protection/Propagation program for the Amami Thrush. www.env.go.jp/nature/yasei/hozonho/ootoratugumi.pdf (accessed 22 Jan 2013; in Japanese).

MINISTRY OF THE ENVIRONMENT (MOE). 2002. Threatened wildlife of Japan–Red Data Book Second Edition–Volume 2, Aves. Japan Wildlife Research Center, Tokyo, Japan (in Japanese).

MINISTRY OF THE ENVIRONMENT (MOE). 2006. Revisions of the Red List of birds, amphibians, reptiles, and invertebrates. www.env.go.jp/press/press.php?serial=7849 (accessed 22 Jan 2013; in Japanese).

MINISTRY OF THE ENVIRONMENT (MOE). 2012. Announcement of the 1st meeting on the designation and management of national parks in the Amami area. kyushu.env.go.jp/naha/pre_2012/0110a.html (accessed 22 Jan 2013; in Japanese).

NEWTON, I. 1998. Population limitation in birds. Academic Press, San Diego, USA and London, UK.

R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RODRÍGUEZ, F. AND Á. C. MORENO. 2008. Breeding biology of the endangered Blue Chaffinch *Fringilla teydea polatzeki* in Gran Canaria (Canary Islands). Acta Ornithologica 43:207–215.

SEILER, A. 2001. Ecological effects of roads: a review. Introductory Research Essay No 9. Swedish University of Agricultural Sciences. Department of Conservation Biology, SLU, Uppsala, Sweden.

SUGIMURA, K. 1988. The role of government subsidies in the population decline of some unique wildlife species on Amami Oshima, Japan. Environmental Conservation 15:49–57.

TAKASHI, M., K. FUJIMOTO, K. KAWAGUCH, H. KAWAGUCHI, AND K. ISHIDA. 2002. The first observation of breeding progress of the critically endangered Amami Thrush *Zoothera major*. Strix 20:71–77 (in Japanese).

THE ORNITHOLOGICAL SOCIETY OF JAPAN. 2012. Chek-list of Japanese birds, Seventh revised Edition. The Ornithological Society of Japan, Sanda, Japan.

YAMASHINA, Y. 1941. Nihon no Chourui to Sono Seitai II. Iwanami-shoten, Tokyo, Japan (in Japanese).

ZHANG, L, S. NURVIANTO, AND R. HARRISON. 2009. Factors affecting the distribution and abundance of *Asplenium nidus* L. in a tropical lowland rain forest in peninsular Malaysia. Biotropica 42:464–469.

The Wilson Journal of Ornithology 126(2):305–320, 2014

NORTHERN SAW-WHET OWL: REGIONAL PATTERNS FOR FALL MIGRATION AND DEMOGRAPHICS REVEALED BY BANDING DATA

JOHN L. CONFER,[1,2] L. LEANN KANDA,[1] AND IREYENA LI[1]

ABSTRACT.—We describe attributes of Northern Saw-whet Owls (*Aegolius acadicus*) during fall migration using 167,774 records from the U.S. Bird Banding Laboratory for central and eastern North America from 1929–2010. We describe movement among 18 geographic regions using records of 1,444 birds captured and recaptured between 1 September and 31 December of the same year. These data show little exchange between western Lake Superior and eastern North America. The direction of movement within a region was strongly influenced by large water bodies, varied greatly among regions, and showed high dispersal in the absence of shorelines of large water bodies. We used recent banding data to analyze population demographics from northwestern Minnesota to the coast of Maine in the north, and from southern Minnesota and southern Wisconsin to southern Appalachia and the mid-Atlantic coastal region in eastern United States. The weighted mean proportion of Hatch Year (HY) birds declined significantly from 63% in northwestern Minnesota to 42% in southern Minnesota/southern Wisconsin and from 70% in northern Ontario to 48% in southern Appalachia. Annual variation in the proportion of HY birds showed little correlation between eastern and central origin sites but moderate correlation within each of these regions. We define irruptions as years when the proportion of HY birds is 15% or greater than the weighted mean for each site, a level that occurs once in 4 years on average but at irregular intervals. We determined a very high correlation between the proportion of HY birds banded in northeast of Lake Ontario and the abundance of small mammals, suggesting a close relationship between food supply and reproductive success. *Received 16 January 2013. Accepted 10 January 2014.*

Key words: *Aegolius acadicus*, age-related migration, fall migration patterns, irruptions, localized migration movements, Northern Saw-whet Owl, regional reproduction patterns.

The breeding range of the Northern Saw-whet Owl *(Aegolius acadicus)* is widely distributed in boreal and northern hardwood forests of Canada and northern United States and extends southward into Mexico and at higher elevations in western North America. The bird is small and nocturnal, and much of the breeding population is in areas of low human density. Consequently, there is still much to learn about their movements, distribution, behavior, and breeding biology (Rasmussen et al. 2008). The number of Northern Saw-whet Owls that are banded during fall migration varies widely from year to year (Rasmussen et al. 2008). Years with particularly high numbers are often called irruption years and are usually related to a high proportion of hatch year (HY) birds (Iliff 2000, Whalen and Watts 2002, Rasmussen et al. 2008).

Recent banding efforts provide data on the age and sex of about 11,000 birds a year (U.S. Geological Survey's Bird Banding Laboratory, hereafter BBL). Using 10 years of recent banding data, Beckett and Proudfoot (2011) documented that Northern Saw-whet Owls move southward an average of one degree latitude every 3.8 days throughout eastern North America during fall migration. Using bands of latitude, they found that the rate, direction, and distance of migration were similar for all ages. Their analyses suggest that that the direction of movement for birds in the Appalachian Forests and the Atlantic seaboard are similar to but different from movement in the Great Lakes Basin.

Here we provide a more detailed description of directional movement and population attributes for smaller geographic regions in eastern and central North America using banding data. Our primary objective was to quantify the patterns of movement by Northern Saw-whet Owls during fall migration. We used GIS to determine the movement lines between capture and recapture sites, and used these lines to describe the patterns of movement among and within ecoregions.

We examined demographic attributes for birds banded in five areas nearer the start of fall migration than any other regions with large numbers of banded birds. These origin sites sample portions of the breeding population from Manitoba to the Maritime Provinces. For comparison, we examined demographic attributes of birds banded in regions near the end of fall migration. Our analyses test if demographic attributes vary at different points during migration, if annual differences in the proportion of HY

[1] Department of Biology, Ithaca College, Ithaca, NY 14850, USA.
[2] Corresponding author; e-mail: confer@ithaca.edu

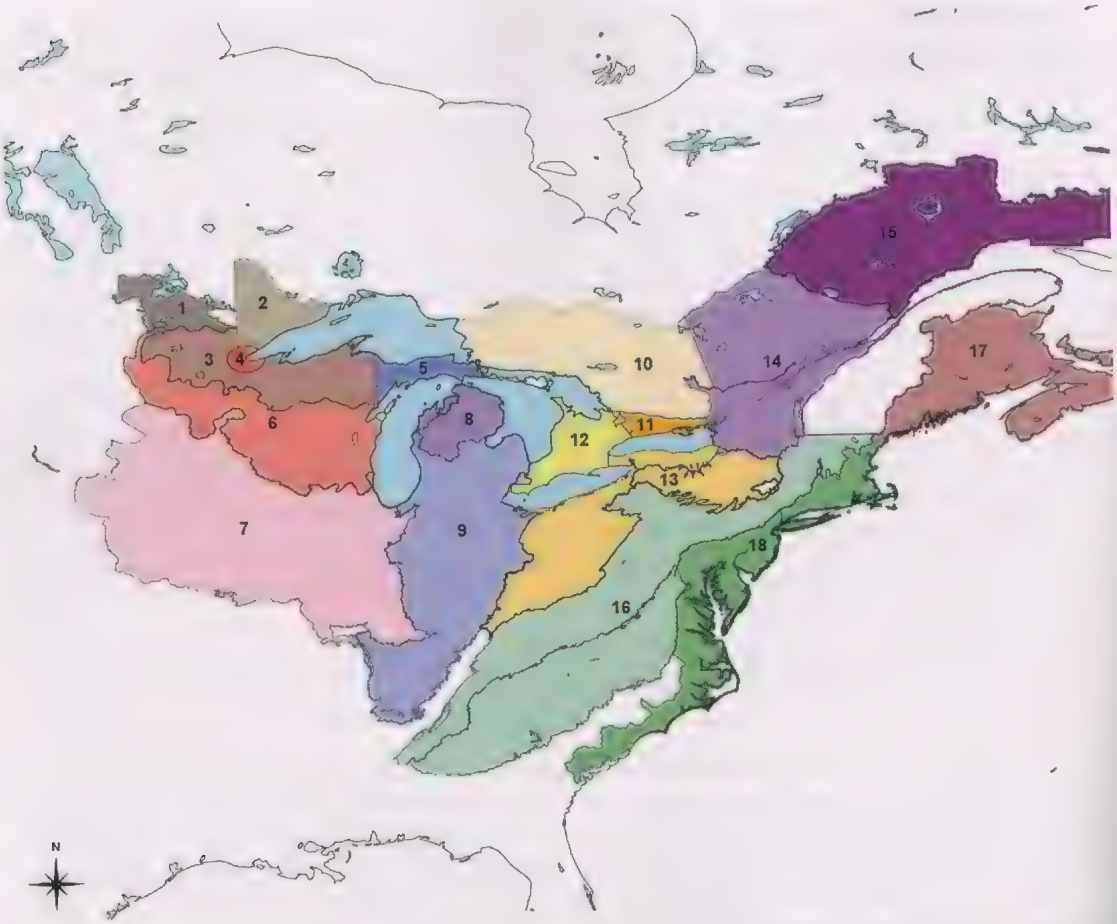


FIG. 1. Ecoregion boundaries adapted from the U.S. Environmental Protection Agency. Names and region boundary descriptions are noted in Table 1.

birds are synchronous for different portions of the breeding range, if particularly high proportions of HY birds occur at a regular interval, and if the proportion of HY birds correlates with abundance of small mammals.

METHODS

Mapping Movements.—The BBL provided banding data for over 206,000 Northern Saw-whet Owls banded in North America between 1929–2010 as well as the re-encounter data for the same time span (4,642 events). A total of 180,894 Northern Saw-whet Owls were banded within our study region encompassing central and eastern North America. Of the total banded in fall (n = 167,774), 1,444 birds were banded and recaptured between 1 September and 31 December of the same year. Data sets were constructed using Structured Query Language (SQL) queries on the BBL tables that were imported into PostgreSQL V8.3 (PostgreSQL Global Development Group 2008).

Using QGIS V1.7.3 (Quantum GIS Development Team 2011) we superimposed lines for the net movement between locations for each owl on Level II or Level III ecoregions described by the U.S. Environmental Protection Agency (EPA; www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm#Level II). Contiguous ecoregions with similar conditions were merged into single units. Some ecoregions were split so that movement patterns around the Great Lakes could be described. Modifications of the EPA ecoregions resulted in 18 geographic regions for central and eastern North America (Fig. 1). Table 1 describes the modifications of the EPA ecoregions and provides the abbreviations for each region used in this text.

Once banding and recapture sites were digitally associated with these regions, we exported the region-specific banding and encounter tables from

TABLE 1. Definitions of level III ecoregions. Boundaries based on U.S. Environmental Protection Agency's online database at www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm with stated modifications.

Figure 1 label	Region name	Ecoregion reference	Modifications to ecoregion boundaries
1	NW MN	5.2.2 Northern Minnesota Wetlands	
2	NW Lake Superior	5.2.1 Northern Lakes and Forests	North and East of Duluth
3	Central MN/N WI	5.2.1 Northern Lakes and Forests	West and South of Duluth, East to Lake Michigan (longitude 87.65°W)
4	Duluth MN	5.2.1 Northern Lakes and Forests	50 km radius of western tip of Lake Superior
5	Upper Peninsula	5.2.1 Northern Lakes and Forests	South of Lake Superior, North of Lake Michigan
6	S MN/S WI	8.1.4 Northern Central Hardwood Forests 8.1.5 Driftless Area 8.2.1 Southeastern Wisconsin Till Plains	
7	Corn Belt	8.2.3 Central Corn Belt Plain 8.3.2 Interior River Valley and Hills 9.2.3 Western Corn Belt Plains 9.2.4 Central Irregular Plains	
8	N Lower Peninsula	5.2.1 Northern Lakes and Forests 8.1.4 Northern Central Hardwood Forests	
9	IN/S MI/W OH	8.1.6 Southern Michigan/Northern Indiana Drift Plains 8.2.2 Huron/Erie Lake Plains 8.2.4 Eastern Corn Belt Plains 8.3.3 Interior Plateau	
10	N Ontario	5.2.3 Algonquin/Southern Laurentians	West of longitude 76.5°W
11	NE Lake Ontario	8.1.1 Eastern Great Lakes Lowlands	East of Lake Simcoe; West of longitude 76.37°W
12	SW Ontario	8.1.1 Eastern Great Lakes Lowlands 8.1.2 Lake Erie Lowland	West of Lake Simcoe; West of southeastern tip of Lake Ontario
13	NY/OH	8.1.2 Lake Erie Lowland 8.1.3 Northern Allegheny Plateau 8.4.3 Western Allegheny Plateau	South of Lake Ontario
14	S Quebec/NE NY	5.2.3 Algonquin/Southern Laurentians 5.3.1 Northern Appalachian and Atlantic Maritime Highlands 8.1.1 Eastern Great Lakes Lowlands	East of longitude 76.5°W; West of longitude 76.37°W
15	St. Lawrence	5.1.3 Central Laurentians and Mecatina Plateau	
16	S Appalachia	5.3.1 Northern Appalachian and Atlantic Maritime Highlands 5.3.3 North Central Appalachians 8.1.7 Northeastern Coastal Zone 8.3.1 Northern Piedmont 8.3.4 Piedmont 8.4.1 Ridge and Valley 8.4.4 Blue Ridge 8.4.2 Central Appalachians	South of latitude 43.82°N; Northern Piedmont Southwest of longitude 77.40°W
17	N Coast	5.3.1 Northern Appalachian and Atlantic Maritime Highlands 8.1.7 Northeastern Coastal Zone 8.1.8 Acadian Plains and Hills 8.1.9 Maritime Lowlands	North of latitude 43.82°N
18	S Coast	8.1.7 Northeastern Coastal Zone 8.3.1 Northern Piedmont 8.3.5 Southeastern Plains 8.5.1 Middle Atlantic Coastal Plain 8.5.4 Atlantic Coastal Pine Barrens	Southeastern Plains North of latitude 36.47°N; Northern Piedmont East of longitude 77.40°W

QGIS to the PostgreSQL database. We made queries across these tables to identify the number of owls moving within a region and between each pair of regions. For select locations with numerous banding records, we also determined the compass direction and dispersal of the owls. We exported data from QGIS onto Google Earth (Google Inc. 2012) and integrated a compass overlay from Wikimedia commons (Wikimedia 2010).

Population Dynamics.—We used banding data from 2000–2010 to analyze population dynamics. During this time, most banders used an audio lure (Erdman and Brinker 1997) to attract birds and applied standardized criteria to determine age (Weidensaul et al. 2011) and sex (Brinker et al. 1997). Factors that might influence capture efficiency for different ages were approximately constant during this time and comparisons from year to year have greater validity than comparisons based on earlier data (Beckett and Proudfoot 2011). We designated five regions in the extreme northern and northeastern portions of the study area as origin sites, because they are the major banding locations closest to the start of the migratory pathway. These origin sites are: 1) NW Minnesota, 2) NW Lake Superior, 3) N Ontario, 4) St. Lawrence, and 5) N Coast. Analyses of population attributes were based on banding data from these origin sites and three sites farther south along the migration routes, S MN/S WI, S Appalachia, and S Coast. No birds were banded in the NW MN origin site in 2000–2001. We omitted demographic analyses for five other site years because they had < 37 banded birds in a year: two for NW MN, two for St. Lawrence, and one for N Ontario. Such low numbers would have imprecisely reflected population attributes. The average number of captures per remaining site-year was 720, while the two site years with minimal sample size had slightly more than 50 banded birds.

Irruptive years are characterized by an unusual abundance of HY birds (Iliff 2000, Whalen and Watts 2002, Rasmussen et al. 2008). Because we cannot standardize for catch effort, we, and other authors, have discussed irruptions in terms of the proportion of HY birds rather than abundance (Beckett and Proudfoot 2011). To quantitatively define irruptions, we first determined the weighted mean proportion of HY birds for all years for each site. We quantified an irruption as the positive deviation from the regions' weighted mean of a magnitude that occurs once every 4 years averaged for all sites.

We tested if the proportions of HY birds between central origin sites were the same with a paired two-tailed *t*-test. We similarly tested whether eastern origin sites differed from one another. We examined whether winter range sites had reduced proportion of hatch year birds by comparing S Appalachia and S Coast to eastern origin sites and S MN/S WI to central origin sites, with families of paired one-tailed *t*-tests. For all *t*-tests, we used arcsin transformation to normalize the values, and for each family of tests corrected with the Holms variant of the Bonferroni correction. We used Pearson's correlation coefficients to evaluate if annual variations in the proportion of young birds were correlated among sites. Correlation coefficients were considered both before and after family-wise correction.

Bowman et al. (2010) compiled a linear regression between abundance of southern red-backed voles (*Myodes gapperi*, syn. *Clethrionomys gapperi*) and the proportion of HY birds banded along the Lake Erie shore. Vole abundance is expressed as number caught per trap nights (×1,000) in Algonquin Provincial Park, Ontario (45° 30′ 38″ N, 78° 31′ 30″ W). We reanalyzed this data using information from the BBL for NE Lake Ontario in 2000–2006.

RESULTS

Recaptures.—Twenty-five birds were recaptured two or more times, for a total of 1,472 recapture events of 1,444 owls banded and recaptured within the same fall season (Fig. 2). These represent 0.9% of the fall banded birds in central and eastern North America. Capture efforts have been more intensive in recent years, with the majority of fall banded birds banded within the last decade (1929–1999, $n = 72{,}110$; 2000–2010, $n = 95{,}664$). However the same-season recapture rate only modestly increased from 0.7% (1929–1999, $n = 516$) to 1.0% (2000–2010, $n = 928$). About 55% ($n = 808$) of recaptured birds from all years were recaptured in the same ecoregion, and 8.6% ($n = 127$) of the reported recapture events were at the same banding station as the owl's previous capture. Two owls originated outside the study area and were recaptured within it, and 15 owls banded within the study area were recaptured outside the area or were reported in ambiguous coordinates over the Great Lakes.

Migratory Direction.—Regional analyses of capture/recapture lines show a difference between the general direction of migration for birds in

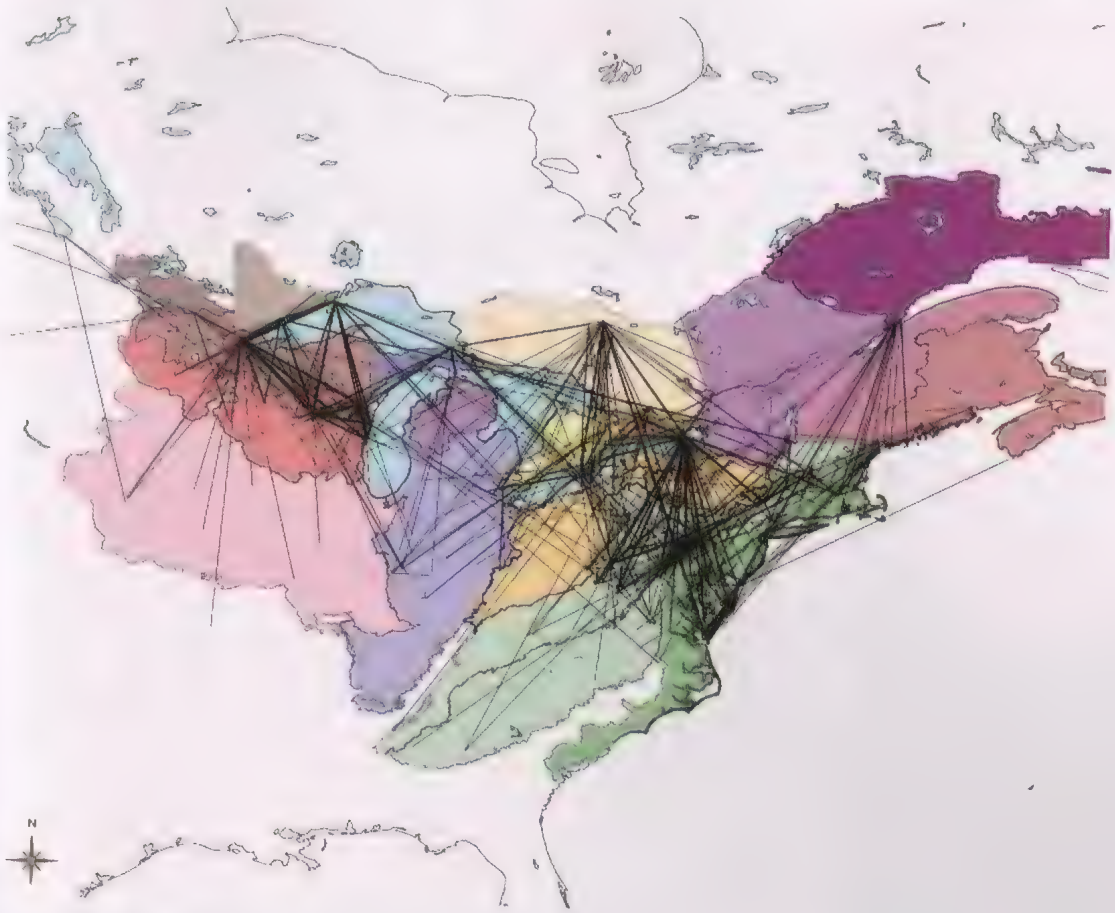


FIG. 2. Geographic locations for 1,444 Northern Saw-whet Owls banded and recaptured during the same fall migrations from 1939–2010. Locations are based on data provided by the USGS Bird Banding Laboratory. Lines are superimposed over defined ecoregions to connect banding sites but do not necessarily represent migratory pathways.

eastern North America and birds in the upper Great Lakes, excepting the influence of large water bodies (Fig. 2). Birds banded in the St. Lawrence region disperse to the southwest with a mean compass direction that is 17° west of due south. In contrast, birds from NW MN disperse southeast with a mean compass direction that is 29° east of due south, or as much as 39° if one extreme directional line to the southwest is omitted. Birds recaptured near Duluth, MN arrive from both the northwest and the northeast but most depart to the southeast.

Dispersal Pattern.—During fall migration, Northern Saw-whet Owls disperse in a fan-like pattern, if uninfluenced by a large water body (Fig. 2). The mean compass direction for birds banded at N Ontario is almost due south at 178° ± 28°. The mean dispersal direction from St. Lawrence is 197° ± 45°. Prince Edward Point Bird Observatory (PEPtBO) is a major banding site located on a landmass that projects about 20 km southeast into Lake Ontario. Dispersal from PEPtBO is generally southward at 188° ± 53°. Six birds from PEPtBO dispersed northward, showing a reversed migration for some birds that reached the peninsular tip and were surrounded by water in all directions but north.

Observed Patterns in the Upper Great Lakes.—Banding results document a major movement of Northern Saw-whet Owls along the northwestern shoulder of Lake Superior from near Thunder Bay, Ontario to Duluth, Minnesota. Of the 191 birds banded in NW Lake Superior and recaptured anywhere, 53% (n = 102) were recaptured in Duluth MN (Table 2). Thus, at least half of the birds banded along NW Lake Superior appear to continue their migration over land in a southwest course rather than crossing the lake. Of the 131 recaptures of birds banded in Duluth MN, none

TABLE 2. The source and destination of Northern Saw-whet Owls captured and recaptured in the same fall migration. Geographic regions are derived from ecoregions defined by the U.S. Environmental Protection Agency. Values for each destination region are the number of recaptures in the destination from a source (*n*), the percentage of emigrants (percentage of all recaptures from a source region caught in that destination, %E), and the percentage of immigrants (percentage of all recaptures in the destination site from a source region, %I) that these recaptures represent.

Source		Destination																		
		NW Minnesota			NW Lake Superior			Central MN/N WI			Duluth, MN			Upper Peninsula			S MN/S WI			Corn Belt		
Region	Total recaptures	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I
NW Minnesota	10										3	0.30	0.02				6	0.60	0.01			
NW Lake Superior	191				10	0.05	1.00	1	0.01	0.50	102	0.53	0.71	3	0.02	0.27	61	0.32	0.12	1	0.01	0.07
Central MN/N WI	3																3	1.00	0.01			
Duluth, MN	131	1	0.01	1.00				1	0.01	0.50	37	0.28	0.26				80	0.61	0.15	8	0.06	0.57
Upper Peninsula	31													7	0.23	0.64	12	0.39	0.02			
S MN/S WI	366																354	0.97	0.68	3	0.01	0.21
Cornbelt	0																					
Lower Peninsula	0																					
IN/S MI/W OH	9																1	0.11	0.00			
N Ontario	69													1	0.01	0.09	2	0.03	0.00			
NE Lake Ontario	119																					
SW Ontario	137																			1	0.01	0.07
NY/OH	9																					
S Quebec/NE NY	20																					
St. Lawrence	21																					
S Appalachia	169																					
N Coast	32																					
S Coast	153																					
Outside Study Area	2										1	N/A	0.01							1	N/A	0.07
Total Recaptures	1,472	1			10			2			143			11			519			14		

TABLE 2. Continued.

Source / Region	Total recaptures	Destination: N Lower Peninsula			IN/S MI/W OH			N Ontario			NE Lake Ontario			SW Ontario			NY/OH		
		n	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I
NW Minnesota	10																		
NW Lake Superior	191				3	0.02	0.08				1	0.01	0.03	2	0.01	0.02			
Central MN/N WI	3																		
Duluth, MN	131				1	0.01	0.03				1	0.01	0.03				1	0.01	0.03
Upper Peninsula	31	2	0.07	1.00	2	0.07	0.05				2	0.07	0.06	3	0.10	0.02			
S MN/S WI	366				5	0.01	0.13												
Corn Belt	0																		
N Lower Peninsula	0																		
IN/S MI/W OH	9				6	0.67	0.15												
N Ontario	69				7	0.10	0.18	1	0.014	1	8	0.12	0.25	21	0.30	0.16	5	0.07	0.14
NE Lake Ontario	119				3	0.03	0.08				15	0.13	0.47	13	0.11	0.10	6	0.05	0.17
SW Ontario	137				12	0.09	0.30				3	0.02	0.09	89	0.65	0.68	15	0.11	0.42
NY/OH	9																1	0.11	0.03
S Quebec/NE NY	20				1	0.05	0.03				2	0.10	0.06				3	0.15	0.08
St. Lawrence	21													2	0.10	0.02			
S Appalachia	169																4	0.02	0.11
N Coast	32																1	0.03	0.03
S Coast	153													1	0.01	0.01			
Outside Study Area	2																		
Total Recaptures	1,472	2			40			1			32			131			36		

TABLE 2. Continued.

Source		Destination																	
		S Quebec/NE NY			St. Lawrence			S Appalachia			N Coast			S Coast			Outside study area[a]		
Region	Total recaptures	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I	*n*	%E	%I
NW Minnesota	10																1	0.10	N/A
NW Lake Superior	191	3	0.02	0.38				3	0.02	0.01							1	0.01	
Central MN/N WI	3																		
Duluth, MN	131																1	0.01	N/A
Upper Peninsula	31							2	0.07	0.01				1	0.03	0.00			
S MN/S WI	366							1	0.00	0.00							3	0.01	
Corn Belt	0																		
N Lower Peninsula	0																		
IN/S MI/W OH	9							1	0.11	0.00							1	0.11	
N Ontario	69	2	0.03	0.25				15	0.22	0.06				6	0.09	0.03	1	0.01	N/A
NE Lake Ontario	119	1	0.01	0.13				57	0.48	0.22				23	0.19	0.10	1	0.01	
SW Ontario	137							12	0.09	0.05				1	0.01	0.00	4	0.03	N/A
NY/OH	9							7	0.78	0.03				1	0.11	0.00			
S Quebec/NE NY	20	1	0.05	0.13				11	0.55	0.04				2	0.10	0.01			
St. Lawrence	21							2	0.10	0.01	4	0.19	0.24	13	0.62	0.06			
S Appalachia	169							136	0.81	0.51				29	0.17	0.13			
N Coast	32	1	0.03	0.13				6	0.19	0.02	13	0.41	0.77	11	0.34	0.05			
S Coast	153							12	0.08	0.05				138	0.90	0.61	2	0.01	
Outside Study Area	2																		
Total Recaptures	1,472	8			0			265			17			225			15		

[a] Of the 15 owls recaptured outside the study area, 7 had ambiguous coordinates that placed them over water in the Great Lakes.

were recaptured in NW Lake Superior, so that few if any birds that reach Duluth MN leave the Duluth area in a northeast direction. Of the birds banded in NW Lake Superior and recaptured anywhere, 32% (n = 61) were re-encountered in S MN/S WI.

Out of a total of 335 birds banded in the northwestern portion of our study area, i.e., NW MN, NW Lake Superior, Duluth MN, and central MN/N WI, and recaptured anywhere, 46% (n = 155) were recaptured within the same four regions. Of the 180 birds banded in but recaptured outside the northwestern portion of our study area, 83% (n = 150) were recaptured to the south and southeast in S MN/S WI. Of the 165 banded immigrants captured in S MN/S WI, 91% (n = 150) came from the northwestern portion of our study area. A few birds entered S MN/S WI from either the Upper Peninsula (n = 12) or even as far away as N Ontario (n = 2). Of 366 birds banded in S MN/S WI and recaptured anywhere, 97% (n = 354) were recaptured in the same ecoregion. Combining the northwestern portion and S MN/S WI, only 6% (n = 42) of the 701 birds banded in the western Upper Great Lakes and recaptured anywhere were recaptured outside the region. Two percent (n = 12) were recaptured farther south in the Corn Belt, 1% (n = 9) angled their migration to the southeast and were recaptured in IN/S MI/W OH, and less than 1% (n = 3) were recaptured as far to the southeast as S Appalachia.

Observed Patterns in the Lower Great Lakes.—The Lower Great Lakes consists of our NE Lake Ontario and SW Ontario regions. There is only one major banding station located to the north of the Lower Great Lakes, the N Ontario origin site. Of all recaptures from N Ontario (n = 69), 12% (n = 8) were recaptured in NE Lake Ontario and 30% (n = 21) were recaptured in SW Ontario. In addition, 22% (n = 15) were recaptured in S Appalachia and 9% (n = 6) in the S Coast, presumably having passed through the Lower Great Lakes.

Of all banded birds recaptured in the Lower Great Lakes (n = 43), 67% (n = 29) came from N Ontario. Another 21% (n = 9) came from the northwest consisting of five birds from the Upper Peninsula and four from NW Lake Superior and Duluth MN. Only four recaptures came from the northeastern portion of the study area with two from St. Lawrence and two from S Quebec/NE NY.

Contrasting NE Lake Ontario and SW Ontario, 11% (n = 13) of the recaptures from birds banded in NE Lake Ontario were recaptured in SW Ontario after migrating primarily to the southwest while only 2% (n = 3) of the birds banded in SW Ontario were recaptured in NE Lake Ontario after migrating primarily to the northeast. Of the recaptures of birds banded in NE Lake Ontario, 13% (n = 119) were recaptured in NE Lake Ontario, while 65% (n = 137) of the recaptures of birds banded in SW Ontario were recaptured in SW Ontario. Of the recaptures of birds banded in NE Lake Ontario, only 5% (n = 6) were obtained in the New York/Ohio region, while 11% (n = 15) of the recaptures from SW Ontario were obtained in the New York/Ohio region. Two-thirds of the recaptures of birds banded in NE Lake Ontario (67%, n = 90) were recaptured in S Appalachia and the S Coast, but only 10% (n = 13) of the recaptures from SW Ontario were recaptured in these regions. Of all the birds banded in the Lower Great Lakes and recaptured outside of the Lower Great Lakes, 71% (n = 103) were recaptured to the south in S Appalachia and S Coast.

Observed Patterns in Southern Appalachia.—Of all birds banded in S Appalachia and recaptured anywhere, 81% (n = 136 of 169) were recaptured within S Appalachia. An additional 17% (n = 29) were recaptured to the south on the nearby S Coast. Birds that were recaptured in S Appalachia came from much of our study area. These included 22% (n = 15) of all recaptures from N Ontario (n = 69), 10% (n = 2) of all recaptures from St. Lawrence (n = 21), 19% (n = 6) of all recaptures from N Coast (n = 32), and even 2% (n = 3) of all recaptures from NW Lake Superior (n = 191), but none from as far northwest as NW MN. None of the 169 recaptures of birds banded in S Appalachia were recaptured in the same fall in any of the origin sites.

Observed Patterns on the Southern Coast.—Of all birds banded on S Coast and recaptured anywhere, 90% (n = 138 of 153) were recaptured on S Coast. S Coast also recaptured 87 birds that were banded outside of this region. These included 9% (n = 6) of all recaptures from N Ontario, a distinctively high 62% (n = 13) of all recaptures from St. Lawrence, which contrasts with S Appalachia with only two recaptures from St. Lawrence, and 34% (n = 11) of all recaptures from N Coast. Of all the recaptures on

TABLE 3. The proportion of Hatch Year birds by site and year. The data include the total banded for each site and for all sites and the proportion of HY birds for the total banded for all years at each site. Site years with fewer than 37 banded birds were omitted.

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total	% HY
NM MN					0.56	0.51	0.78[a]	0.56	0.49	0.72	0.68	1,980	0.63
NW L. Superior	0.61	0.68	0.75[a]	0.72[a]	0.45	0.45	0.71[a]	0.56	0.27	0.60	0.71[a]	8,609	0.60
S MN/S WI	0.41	0.35	0.39	0.48	0.34	0.36	0.52[a]	0.38	0.23	0.42	0.57[a]	12,813	0.42
N Ontario	0.27	0.66	0.64	0.78	0.64	0.63	0.76	0.85[a]	0.45	0.50		5,392	0.70
St. Lawrence	0.25	0.70		0.54	0.59		0.64	0.87[a]	0.26	0.69	0.71	1,169	0.67
N Coast	0.20	0.76[a]	0.49	0.70[a]	0.38	0.58	0.48	0.66[a]	0.14	0.60[a]	0.80[a]	2,612	0.52
S Appalachia	0.34	0.62[a]	0.42	0.49	0.38	0.38	0.53	0.63[a]	0.14	0.51	0.59[a]	16,068	0.48
S Coast	0.32	0.76[a]	0.57	0.64	0.42	0.71	0.51	0.75[a]	0.27	0.55	0.61	9,705	0.62
Overall % HY	0.34	0.65	0.55	0.62	0.47	0.52	0.62	0.66	0.28	0.57	0.67	58,348	0.54

[a] Indicates site year with %HY ≥15% above site mean.

S. Coast, only one bird came from central North America.

Regions of Origin.—Our study area encompasses banding sites from Manitoba to the Canadian Maritime Provinces, an arc of about 2,500 km. Of the five origin sites, only the St. Lawrence contributed recaptures to any other origin site. This consists of four birds (0.3%) out of 1,231 banded in St. Lawrence, all of which were recaptured on N Coast. All origin sites were located to the north or northeast of all other regions that had a large number of banded birds. There is a large spatial segregation between each of them and a near total absence of capture/recaptures among them. Subsequently, we analyze the population dynamics of each origin site independently.

Population Dynamics.—The mean proportion of HY birds from 2000–2010 of all birds banded at each site ranged from 0.42 for S MN/S WI to 0.70 for N Ontario with a mean of 0.54 for all site years (Table 3). In the central sites, the proportion of HY birds was significantly higher in NW Minnesota than in NW Lake Superior (paired 2-tailed *t*-test, $n = 14$, $t = 2.611$, $P = 0.040$) while S MN/S WI had a significantly lower proportion of HY birds than both NW Minnesota and NW Lake Superior (paired 1-tailed *t*-tests, $n = 14$, $t = -7.612$, $P < 0.001$, and $n = 22$, $t = -6.165$, $P < 0.001$, respectively). In the east, the N Coast trended to a lower proportion of HY birds than in N Ontario, but this was not significant after family-wise correction (paired 2-tailed *t*-test, $n = 21$, $t = 2.554$, $P = 0.031$). The site at St. Lawrence was not different from either of the other eastern origin sites (paired 2-tailed *t*-tests; N Coast $n = 18$, $t = 1.158$, $P = 0.28$; N Ontario $n = 16$, $t = 0.905$, $P = 0.40$).

The proportion of HY birds for S Appalachia was distinctly lower than the proportions for all three eastern origin sites even after family-wise correction (paired 1-tailed *t*-tests; N Coast $n = 22$, $t = -2.148$, $P = 0.029$; St. Lawrence $n = 18$, $t = -3.409$, $P = 0.005$; N Ontario $n = 20$, $t = -4.208$, $P = 0.001$). S Coast HY proportions do not differ significantly from N Coast, St Lawrence, or N Ontario (paired 1-tailed *t*-tests; N Coast $n = 22$, $t = 0.738$, $P = 0.76$; St. Lawrence $n = 18$, $t = -1.423$, $P = 0.096$; N Ontario $n = 20$, $t = -1.663$, $P = 0.065$).

Perhaps the most striking attribute of the demographic values is the extremely low recruitment for 2000 and 2008 (Table 3). In 2000, the values for the eastern sites were the lowest or next to lowest of all years, and in 2008 the values for all eastern and both central sites alternated with 2000 as the lowest or next to lowest of all years.

Pearson's correlation coefficients suggest that the two central origin sites are significantly correlated to each other ($r = 0.87$) and to S MN/S WI (NW Minnesota $r = 0.78$; NW Lake Superior $r = 0.82$) although none of these remain significant with a family-wise correction (Table 4). The central and eastern sites that are closest to each other, NW Lake Superior and N Ontario, have a low correlation coefficient of 0.34. All other correlations between central and eastern origin sites range from 0.20–0.60 and are also non-significant. Between each pair of eastern sites, the correlation coefficients range from 0.72–0.83. These correlations are not statistically significant with a family-wise correction but suggest a significant correlation as single comparisons. This inconsistent detection of a significant correlation suggests at best only a moderate correlation in

TABLE 4. Pearson's correlation coefficients (r) compare annual proportion of HY birds for five origin sites and three wintering sites.

	NW Minnesota	NW Lake Superior	S MN/S WI	N Ontario	St. Lawrence	N Coast	S Appalachia
NW Lake Superior	0.87[a]						
S MN/S WI	0.82[a]	0.78[a]					
N Ontario	0.20	0.34	0.36				
St. Lawrence	0.43	0.47	0.39	0.78[a]			
N Coast	0.43	0.60	0.55	0.72[a]	0.83[a]		
S Appalachia	0.61	0.71[a]	0.62[a]	0.65[a]	0.89[b]	0.87[b]	
S Coast	0.10	0.45	0.29	0.71[a]	0.86[a]	0.90[b]	0.79[a]

[a] Indicates a statistically significant correlation at $\alpha = 0.05$ for individual comparisons.
[b] Indicates a statistically significant correlation with correction for multiple comparisons.

annual variation in the proportion of HY birds for all years across 1,500 km of the eastern breeding range (Table 4).

Correlations for each of the three eastern origin sites with S Appalachia range from 0.65–0.89, and correlations with S Coast range from 0.71–0.90, all significant independently. Both St. Lawrence and N Coast significantly correlated with S Appalachia, and N Coast significantly correlated with S Coast, even with the high standard of family-wise correction. S Coast and S Appalachia correlate with $r = 0.79$, significant before correction, but S Coast correlates poorly with all western sites with correlations ranging from 0.10–0.45. NW Lake Superior and S MN/S WI are each moderately correlated to S Appalachia ($r = 0.71$ and 0.62, respectively, significant only before correction).

The literature on Northern Saw-whet Owls commonly considers irruptions. Despite this interest, there has been no quantitative definition of an irruption. A review by Rasmussen et al. (2008) suggested that irruptions occur about once in every 4 years and we apply this frequency to derive a quantitative lower boundary for an irruption year. The weighted mean proportion of HY birds for each site varies considerably from lows of 42% for S MN/S WI and 48% for S Appalachia to 70% for N Ontario (Table 3). Consequently, no single value can define an irruption for all sites. We define an irruption in relation to the mean proportion of HY birds for each site. For all 81 site years in our study, the proportion of HY birds was ≥15% above the weighted site mean for each site in one of four site years. To convert the commonly described frequency for irruptions to a quantitative value, we define an irruption as a year when the proportion of HY birds equals or exceeds 115% of the long term, weighted mean for a site. Among our sites, the frequency of irruptions were as follows: NW MN – once in 7 years, NW Lake Superior – 4 times in 11 years with observed intervals of 1, 3, and 4 years, S MN/S WI – twice in 11 years with an interval of 4 years, N Ontario – once in 10 years with at least 7 years without an irruption, St. Lawrence – once in 9 years, N Coast –5 times in 11 years with observed intervals of 2, 4, 2 and 1 year(s), S Appalachia – 3 times in 11 years with observed intervals of 6 and 3 years, and S Coast – twice in 11 years with an observed interval of 5 years.

Prey Abundance and Owl Recruitment.—Bowman et al. (2010) compared abundance of red-backed voles to the proportion of HY owls banded along the Lake Erie shore about 380 km from the trapping site, which provided an r^2 value of only 0.22. We reanalyzed the vole data with BBL data for 4,709 owls banded in NE Lake Ontario with major banding sites that are ~150 km southwest and ~230 km southeast of the small mammal traplines. The annual deviation from the mean proportion of HY birds for NE Ontario compared to the vole abundance shows a very strong correlation with an r^2 value of 0.81 for the 6 years of data that overlap with these two studies.

DISCUSSION

Our analyses make extensive use of capture/recapture data, which must be interpreted with caution for several reasons. Straight lines that connect capture/recapture points indicate the net movement but do not establish the actual migratory path. Migratory patterns suggested by capture/recapture lines are highly influenced by the non-random distribution of banding effort. For example, the capture of a large number of migrants by a shoreline banding station may

accurately reflect the localized abundance of birds but locating many stations on the shoreline overrepresents that local abundance. Conversely, a small number of capture/recaptures in some regions may be because of a limited banding effort or few birds in that region or likely both. The recapture site probably is not the end point of migration since most birds are captured while migrating. Despite these limitations, capture/recapture data reveal distinct patterns about Northern Saw-whet Owls' migration.

Migratory Patterns.—S MN/S WI, S Appalachia, and S Coast had within-region recapture rates of 81–97%. These high recapture rates provide strong inference that most birds banded in these regions stayed there for the winter (Whalen and Watts 2002). SW Ontario also had a very high percentage of recaptures within the region. However, there is a distinct concentration of major banding stations along Lake Erie's shore (Beckett and Proudfoot 2011). In this instance, the high recapture rate may be partially because of a concentration of banding stations and birds along a narrow migratory route.

Capture/recapture lines show that Northern Saw-whet Owls in central and eastern North America are generally divided into two populations. The population from the northwestern portion of the Upper Great Lakes winters primarily in S MN/S WI. Only a small percentage of birds from the western Upper Great Lakes are recaptured farther south in the Corn Belt or southeast in IN/S MI/W OH, although sparse trapping efforts in these two regions may underrepresent these areas as wintering regions. However, the low recapture of birds from the western Upper Great Lakes in S Appalachia, which has a high capture effort, supports that few birds originating from the western Upper Great Lakes move that far east to winter. Similarly, none were captured in the highly monitored S Coast, although Erdman et al. (1997) reported one fall trans-Appalachian migrant banded in S MN/S WI and recaptured in Halifax, NC, which fell just outside of our study area.

The low correlation coefficient for the proportion of HY birds between NW Lake Superior and N Ontario also suggests there is little mixing of the breeding populations from central and eastern North America during fall migration. Northwest Lake Superior and S MN/WI do show at least moderate correlation in HY proportion with S Appalachia; however, the very low number of capture/recaptures that occur between these heavily trapped areas suggests that few birds from the northwest side of Lake Superior mix with the eastern portions of our study area from summer through winter. Few Northern Saw-whet Owls are banded from the northernmost point of Lake Superior to the northeast of Lake Superior; given the wide angle of dispersion seen at other banding stations it is possible that birds breeding in this portion of Ontario may split into two migratory paths, one west around Lake Superior and wintering west of Lake Michigan, and a second path moving east along the northeastern shore of Lake Superior to join eastern-origin birds funneling through the Lower Great Lakes. Much could be learned about potential mixing between the central and eastern populations if there were banding stations along the northeastern shorelines of the Upper Great Lakes between NW Lake Superior and N Ontario. Spring migration patterns, which we did not consider, may be different.

In addition to the large number of birds that are banded in NW Lake Superior and recaptured in Duluth MN, another 61 birds banded in NW Lake Superior were recaptured in S MN/S WI providing capture/recapture lines that cross Lake Superior (Fig. 2). Erdman et al. (1997) recognized that such a recapture would not distinguish between a bird that migrated southwest paralleling the shoreline to Duluth and then turned to the southeast to, for example, Green Bay, WI for a distance of 580 km, or flew across Lake Superior to Green Bay for a straight line distance of 400 km. Without direct tracking of movement paths, we still do not know what proportion of birds fly the more circuitous land versus the shorter water route.

There is a moderate difference in the general direction of movement from SW Ontario in comparison to NE Lake Ontario. A proportion of birds banded in SW Ontario continue southwest and are recaptured in New York/Ohio while a decidedly higher proportion of birds banded in NE Lake Ontario continue in a more southern direction toward S Appalachia and S Coast.

Johnson and Anderson (2003) suggested a major migratory route from central Ontario down the Ohio River Valley to Kentucky, although they provided no reference for this proposal. Others have referred to this as a major route (Rasmussen et al. 2008, Brittain 2009) while referencing only Johnson and Anderson (2003). There have been

few banders in the region, and movement of a large number of birds through the Ohio River Valley is not supported by numerous capture/recapture lines (Table 2). The existing banding effort shows that 71% ($n = 103$) of the recaptures from SW Ontario and NE Lake Ontario migrate southward to S Appalachia and S Coast with a smaller number of recaptures in NY/OH and IN/S WI/W OH (25%, $n = 36$).

Our analyses of movement lines reinforce the well-documented perspective that many Northern Saw-whet Owls migrate to and winter in the Appalachian Forests and southern coastal areas (Rasmussen et al. 2008), but provide greater detail about this movement. Comparing S Appalachia and S Coast, the S Appalachia obtains a higher proportion of all the recaptures from N Ontario while S Coast obtains a much higher proportion of the recaptures from St. Lawrence. S Coast also obtains a high proportion of the recaptures from the N Coast as might be expected while birds continue a coastal migration route (Holroyd and Woods 1975).

Population Dynamics.—Irruptions occurred at one or more eastern origin sites in 5 different years of the 11 years examined. However, irruptions were detected in only 3 years in S Appalachia and only 2 years on S Coast (Table 3). Similarly, irruptions occurred in 4 out of the 11 years of our analyses for the central origin sites but were detected in only 2 years in S MN/S WI. Combining migrants from an origin site that had an irruption with migrants from an origin site without an irruption moderates the variation in the proportion of HY birds at winter sites. Winter sites certainly provide valuable information on factors such as survival, movement patterns, and integrated population trends but are a poor reflection of population dynamics in different breeding regions.

Variations in the proportion of HY birds at the origin sites provide insight about reproductive synchrony across the central and eastern portion of the breeding range. Extremely low recruitment rates for all eastern origin sites in 2000 and for all eastern and central origin sites in 2008 raise the possibility that some controlling factor prevailed across 1,300 km in 2000 and across 2,500 km in 2008. Similar weather conditions could extend over a large distance and could synchronize a bottom-up trophic regulation, potentially related to seed crop and small mammal abundance (Falls et al. 2007). Variations in seed crops have shown a significant correlation across 500 km for most taxa of mixed coniferous and deciduous forests, across 1,000 km for *Pinus*, and have even shown a small but significant level of synchrony among all conifers at >5,000 km (Koenig and Knops 2000).

Overall, synchrony in the proportion of HY birds among origin sites is weak. The correlation coefficients suggest two northwestern origin sites have little synchrony with each of the three eastern origin sites. This asynchrony has been noted previously: in 1995 some eastern banding stations reported multi-fold increases in number caught while banding stations in northwestern reported only a slightly above average capture rate (Brinker et al. 1997). Among the eastern sites, Pearson's *r*-values leave 20–30% of the variation unexplained, suggesting that factor(s) that control recruitment sometimes vary between adjacent regions in the same year. Bowman et al. (2008) sampled small mammals at 60 trap lines concentrated in three areas in central and northern Ontario and found that local peaks in the abundance of small mammals did not extend beyond 200 km. Such localized prey abundance would explain differences in recruitment between adjacent origin sites.

Studies at specific banding sites (Whalen and Watts 2002, Cheveau et al. 2004) support the interpretation (Iliff 2000, Rasmussen et al. 2008) that irruptions occurred approximately every 4 years. These studies of irruptions represent an immense amount of effort by banders but provide only a moderately small sample of years for each site. An unusually good year in a small sample may create the impression that irruptive years differ in kind from other years: the proportion of HY birds varied from 14–80% for the N Coast and from 25–87% for the St Lawrence. However, in our sample of 81 site years, irruptions are part of a continuous variation in reproductive success. There were 15 years when the percentage of HY birds was within 10–20% of the weighted mean. Thus, an irruption is an arbitrary designation useful to recognize a year with very good success.

At three of the origin sites, the intervals between irruptions were from 1–4 years (Table 3). Longer intervals of uncertain duration occurred for NW MN with one irruption in 7 years and for N Ontario with one irruption in 10 years. If irruptions occurred in the first year before and after the documented years for both these sites, the shortest possible intervals would have been 3, 4, 5, and 8 years. Banding in southern Manitoba detected only one year with an irruption, using our

quantitative definition, followed by 7 years without an irruption (De Ruyck 2009) for a minimal interval of 8 years. South-central Indiana obtains birds from both central and eastern North America. After 6 years of banding of this integrated population at three stations, none of the years had a proportion of HY birds that was ≥15% over the mean. Overall, banding data for nearly 20,000 birds from five origin sites with 59 site years and other long term studies show that irruptions occur at highly irregular intervals in central and eastern North America, occasionally even in consecutive years.

N Coast had five irruptive years whereas each of the other two eastern origin sites had only one irruption. This unusually high frequency is affected by the two years when N Coast had the lowest proportion of HY birds of any other eastern origin sites. These values, i.e., 14% and 20%, lowered the weighted mean and made years at N Coast with only moderately high proportions of HY birds scale as an irruption in comparison to the N Coast mean. It is not clear from our sample if the frequency of irruptions for N Coast is intrinsically different from the other origin sites.

A decline in the proportion of HY birds during migration is large and highly consistent for much of central and eastern North America. The proportion of HY birds in S MN/S WI is lower than the proportion for all 18 site years for the northwestern origin sites. The proportion of HY birds in S Appalachia is lower than the proportion for all eastern origin sites for 26 of 30 site years. Three of the four exceptions occurred in 2000 when all three eastern origin sites had extremely low proportions for HY birds (Table 3).

Our analyses do not provide any insight about why the proportion of HY birds declines during migration in some areas. This decrease could result from HY birds that don't migrate as far as older birds, or from a higher predation rate or a higher rate of starvation for young, inexperienced birds, or some combination of these factors.

Beckett and Proudfoot (2011) did not detect any differences in migration by age for all years combined. However, their analyses grouped data by latitude bands. This pools data for birds in different stages of their migration and from different areas. For example, one latitude band combines birds in mid-migration in southern Ontario with birds in S MN/S WI that have reached their winter site (fig. 1 of Beckett and Proudfoot 2011). Pooling these data by latitude bands obscures regional differences.

S Coast does not show a decrease in HY proportion from the major contributing origin sites. The potential influence of the irregularities of coastal shorelines, and the documentation of large differences in the proportion of HY birds among nearby banding sites (van Althuis 2009), and an extraordinary 28-fold difference in the proportion of HY birds between irruptive and non-irruptive years at one site (Whalen and Watts 2002) suggest that analyses of individual banding sites are particularly appropriate for this region.

Prey Abundance.—Food supply may influence the abundance of migratory Northern Saw-whet Owls in at least two ways. Nomadic movements of adult Northern Saw-whet Owls in spring can concentrate breeding birds in regions with an abundance of red-backed voles (Bowman et al. 2010), which could produce a localized abundance of birds during the fall migration. Also, as noted previously, a high abundance of prey sometimes correlates with high reproductive success (Cote et al. 2007, Bowman et al. 2010). This correlation may be masked by local variation in prey abundance. De Ruyck (2009) found that the proportion of HY birds banded in southern Manitoba correlated with data from trapping of small mammals in one location but not another nearby location during 8 years of sampling.

The banding data can be used with previous studies of small mammal abundance to assess relationships between owl recruitment and food supply. As examples, a crash in abundance of red-backed voles in the boreal forests of Quebec in 2000 (Cheveau at al. 2004) correlates with extremely low proportions of young Northern Saw-whet Owls in all our eastern origin sites in that year, while a peak in abundance of both red-backed voles and meadow voles (*Microtus pennsylvanicus*) in Manitoba in 2006 (Swengel et al. 2008) correlates with an unusually high proportion of HY birds in NW MN.

Association between red-backed voles' abundance and the proportion of HY birds banded along the Lake Erie shoreline, however, was weak ($r^2 = 0.22$) (Bowman et al. 2010). Re-analysis of the same mammal data using data for birds banded closer to the mammal trapping site provided a much stronger r^2 value (0.81, Fig. 3). We expected a higher correlation because of the closer proximity, but a value this high is surprising because some of the birds caught in NE Lake Ontario come from throughout most of our study area.

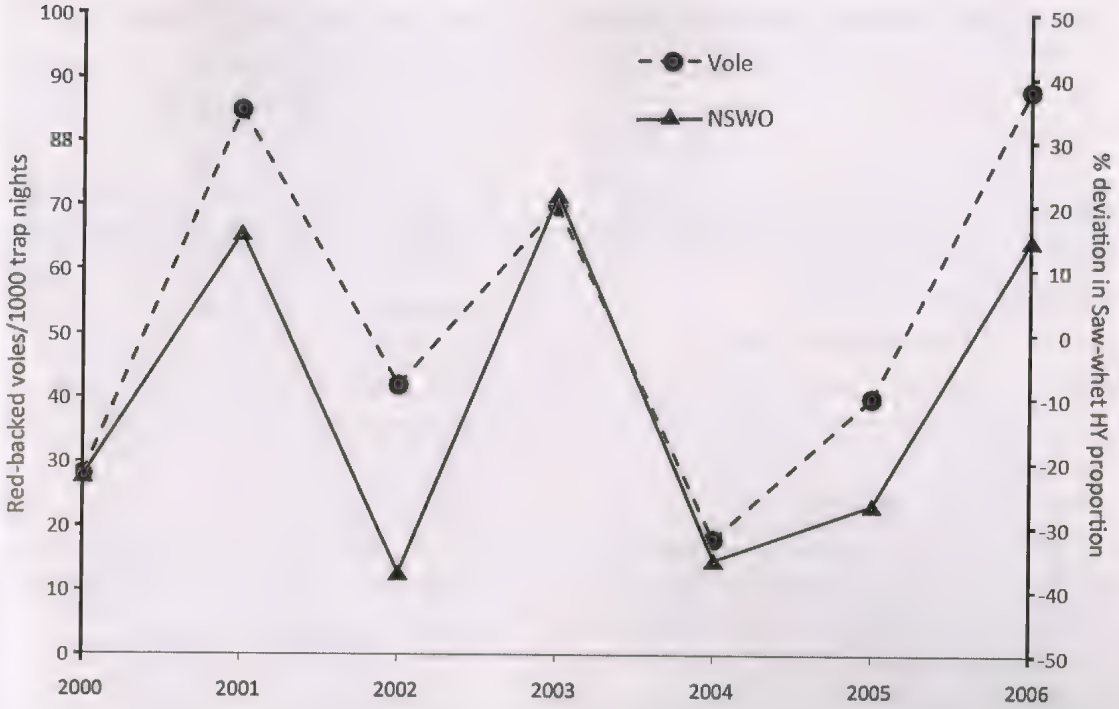


FIG. 3. Red-backed voles and hatch year (HY) Northern Saw-whet Owls in 2000–2006. Vole abundance is expressed as number caught per trap night (×1,000) in Algonquin Provincial Park from figure 4 of Bowman et al. (2010). The deviation in the proportion of HY birds from the mean proportion of HY birds uses BBL data for 4,709 owls banded in northeastern Lake Ontario in 2000–2006 about 250 km south of the trapping site.

A positive relationship between food abundance and the proportion of HY birds among migratory Northern Saw-whet Owls is strongly indicated by existing studies. Regional analyses, which can account for small scale variation, may establish that the proportion of HY birds for Northern Saw-whet Owls may be taken as an indicator of small mammal abundance. It is interesting that the larger Boreal Owl (*Aegolius funereus*) appears to show a contrary response. In northern Europe (Korpimäki 1986) and in Quebec, Canada (Cheveau et al. 2004, Cote at al. 2007) the years with conspicuous southward movement of Boreal Owls were associated with a crash in prey density.

The immense amount of banding data combined with computer-based geographic analyses has allowed us to examine the detail of migratory patterns and demographics for Northern Saw-whet Owls across central and eastern North America. Migratory direction differs greatly even within portions of North America. Reproductive rates differ between central and eastern North America but are similar within these regions, although some differences within these regions do occur. Owl recruitment seems highly correlated with fluctuations in the prey base, but only bad years seem strongly synchronized over a very large area. Further analyses of the multi-level trophic relationships that influence irruptions of Northern Saw-whet Owls at small geographic scale are certainly warranted.

ACKNOWLEDGMENTS

The ecoregion classification of the U.S. Environmental Protection Agency was crucial to the spatial foundation of our analyses. We will provide the digital files for the EPA ecoregion boundaries on request. Data were provided by the U.S. Bird Banding Laboratory with guidance from D. Bystrak and the assistance of M. Rogosky. The great effort of many banders in hundreds of locations provided the data used for analyses of the spatial pattern of migratory movements. The meticulous effort by hundreds of banders to determine age for tens of thousands of birds allowed us to assess population dynamics. Special credit belongs to T. Erdman, whose banding work is exceptional, and who with D. Brinker documented the immense increase in capture efficiency because of the use of audio lures. This seems to have inspired an increase in banding effort. Project Owlnet, initiated and sustained by S. Huy, S. Weidensaul, and D. Brinker, has provided major guidance and encouragement for banding efforts. A seminar by V. Freer and the work of

S. Beckett and G. Proudfoot inspired this study. The encouragement and comments of S. Weidensaul, D. Okines, T. Bowman, A. Swengel, and an anonymous reviewer improved this manuscript. G. Proudfoot provided an exceptionally thorough review that greatly enhanced this manuscript. We are indebted to B. McGuire for his many hours of insightful discussions during owl banding. This study was derived from a research project sponsored by the Department of Environmental Studies and Science at Ithaca College, which together with the Department of Biology at Ithaca College supported this study.

LITERATURE CITED

Beckett, S. R. and G. A. Proudfoot. 2011. Large-scale movement and migration of Northern Saw-whet Owls in North America. Wilson Journal of Ornithology 123:521–535.

Bowman, J., R. D. Phoenix, A. Sugar, F. N. Dawson, and G. Holborn. 2008. Spatial and temporal dynamics of small mammals at a regional scale in Canadian boreal forest. Journal of Mammalogy 89:381–387.

Bowman, J., D. S. Badzinski, and R. J. Brooks. 2010. The numerical response of breeding Northern Saw-whet Owls (*Aegolius acadicus*) suggests nomadism. Journal of Ornithology 151:499–506.

Brinker, D. F. 2000. Sex criteria for Northern Saw-whet Owls. www.projectowlnet.org (accessed 15 Jul 2013).

Brinker, D. F., K. E. Duffy, D. M. Whalen, B. D. Watts, and K. M. Dodge. 1997. Autumn migration of Northern Saw-whet Owls (*Aegolius acadicus*) in the middle Atlantic and northeastern United States: what observations from 1995 suggest. Pages 74–89 *in* Biology and conservation of owls of the northern hemisphere: 2nd international symposium (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Editors). USDA Forest Service General Technical Report NC-190, St. Paul, Minnesota, USA.

Brittain, R. A., J. Vicky, J. Meretsky, J. A. Gwinn, J. G. Hammond, and J. K. Riegel. 2009. Northern Saw-whet Owl (*Aegolius acadicus*) autumn migration magnitude and demographics in south-central Indiana. Journal of Raptor Research 43:199–209.

Cheveau, M., P. Drapeau, I. Imbeau, and Y. Bergeron. 2004. Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. Oikos 107:190–198.

Cote, M., J. Ibarzabal, M.-H. St-Laurent, J. Ferron, and R. Gagnon. 2007. Age dependent response of migrant and resident *Aegolius* owl species to small rodent population fluctuations in the eastern Canadian boreal forest. Journal of Raptor Research 41:16–25.

De Ruyck, C. C. 2009. Northern Saw-whet Owls: Migration and population trends in Manitoba. Thesis. University of Manitoba, Winnipeg, Canada.

Erdman, T. C. and D. F. Brinker. 1997. Increasing mist net captures of migrant Northern Saw-whet Owls (*Aegolius acadicus*) with an audio lure. Pages 533–544 *in* Biology and conservation of owls of the northern hemisphere: 2nd international symposium (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Editors). USDA Forest Service General Technical Report NC-190. St. Paul, Minnesota, USA.

Erdman, T. C., T. O. Meyer, J. H. Smith, and D. M. Erdman. 1997. Autumn populations andmovements of migrant Northern Saw-whet Owls (*Aegolius acadicus*) at Little Suamico, Wisconsin. Pages 167–172 *in* Biology and conservation of owls of the northern hemisphere: 2nd international symposium (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Editors). USDA Forest Service General Technical Report NC-190, St. Paul, Minnesota, USA.

Falls, J. B., E. A. Falls, and J. M. Fryxell. 2007. Fluctuations in deer mice in Ontario in relation to seed crops. Ecological Monographs 77:19–32.

Google, Inc. 2012. Google Earth. Version 6.2. www.google.com/earth/index.html (accessed 15 Jul 2013).

Holroyd, G. L. and J. G. Woods. 1975. Migration of the Northern Saw-whet Owl in eastern North America. Bird Banding 46:101–105.

Iliff, M. 2000. Middle Atlantic region. North American birds 54:36–37.

Johnson, A. and S. H. Anderson. 2003. Conservation assessment for the Northern Saw-whet Owl in the Black Hills National Forest, South Dakota and Wyoming. University of Wyoming, USA.

Koenig, W. D. and J. M. H. Knops. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. American Naturalist 155:59–69.

Korpimäki, E. 1986. Gradients in population fluctuations of Tengmalm's Owl (*Aegolius funerus*) in Europe. Oecologia 69:195–201.

PostgreSQL Global Development Group. 2008. PostgreSQL. Version 8.3 www.postgresql.org (accessed 15 Nov 2011).

Quantum GIS Development Team. 2011. Quantum GIS Geographic Information System. Version 1.7.3. Open Source Geospatial Foundation Project. qgis.osgeo.org (accessed 15 Nov 2011).

Rasmussen, J. L., S. G. Sealy, and R. J. Cannings. 2008. Northern Saw-whet Owl (*Aegolius acadicus*). The birds of North America. Number 42, revised.

Swengel, A. B., J. R. Duncan, and S. R. Swengel. 2008. Auditory surveys for Northern Saw-whet Owls in southern Wisconsin 1986–2006, with comparison to Manitoba owl and mammal surveys. Passenger Pigeon 70:3–18.

U.S. Environmental Protection Agency (EPA). www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm#Level III (accessed 8 Aug 2012).

van Althuis, K. 2009. Migration dynamics of the Northern Saw-whet Owl in the Piedmont, Mountain, and Coastal Plain Provinces of Virginia. Thesis. Liberty University, Lynchburg, Virginia, USA.

Weidensaul, C. S., B. A. Colvin, D. F. Brinker, and J. S. Huy. 2011. Use of ultraviolet light as an aid in age classification of owls. Wilson Journal of Ornithology 123:373–377.

Whalen, D. M. and B. D. Watts. 2002. Annual migration density and stopover patterns of Northern Saw-whet Owls (*Aegolius acadicus*). Auk 119:1154–1161.

Wikimedia Commons. 2010. File: Compass Card.png. commons.wikimedia.org/wiki/File:Compass_Card.png (accessed 1 Aug 2013).

The Wilson Journal of Ornithology 126(2):321–332, 2014

DISTRIBUTION OF COLOR-MORPHS OF THE EASTERN SCREECH-OWL IN IOWA

TEX A. SORDAHL[1]

ABSTRACT.—The distinct rufous and gray color-morphs of the Eastern Screech-Owl (*Megascops asio*) have long intrigued ornithologists. Eastern Screech-Owls range across the eastern half of the United States, where the morph ratio varies from >70% rufous birds in the center of the range to <30% rufous at the periphery. Although the adaptive significance of polymorphism is, in general, poorly understood, careful mapping of the morph-frequency and determination of ratio clines is a first step toward understanding this phenomenon. In this paper, I examine the distribution of Eastern Screech-Owl color-morphs in Iowa, which lies in the northwestern part of the species' range. I collected 519 records of Iowa screech-owls from museum curators, wildlife rehabilitators, bird-banders, and bird watchers. For all records combined, 41.0% were rufous morphs, 55.7% were gray morphs, and 3.3% were intermediates. For all birds of known sex, 44.7% (21/47) of males and 57.6% (34/59) of females were rufous; the difference was not statistically significant, but the results are consistent with a trend in other studies suggesting that females are more likely than males to be rufous. The percentage of rufous screech-owls increased clinally from west to east across Iowa, but did not change from north to south. Because annual precipitation exhibits a longitudinal pattern in Iowa and annual temperature exhibits a latitudinal pattern, this suggests that the morph ratio pattern in Iowa is influenced more by precipitation than by temperature. Based on records dating 1880–2003, the percentage of rufous birds decreased from the early to later decades of the 20th century. The range-wide distribution of morph ratio clines fits a model where rufous morphs are better-adapted at the center of the range but gray morphs are selected for toward the periphery. *Received 29 August 2013. Accepted 10 January 2014.*

Key words: color morph, Eastern Screech-Owl, Iowa, *Megascops asio*, polymorphism.

Polymorphism, the occurrence of strikingly distinct phenotypes within a population, is widespread in the animal kingdom (Mayr 1970). In birds, this type of variation often manifests as color-morphs, and conspicuous examples include many predatory species such as some herons, hawks, and jaegers (Hancock and Kushlan 1984, del Hoyo et al. 1994, Sibley 2000).

Owls (Strigiformes: Tytonidae and Strigidae) are one of the groups of birds in which color polymorphism is common (Huxley 1955, Roulin 2004). Of 250 species of owls worldwide, about 55 (22%) exhibit color polymorphism (König and Weick 2008). Polymorphic owls are usually classified in the categories of either light and dark morphs or rufous, brown, and gray morphs. Light and dark morphs occur in about 17 species of owls, primarily in the genera *Tyto*, *Otus*, and *Ninox*. Rufous, brown, and gray morphs occur in about 38 species, primarily in the genera *Otus*, *Megascops*, *Glaucidium*, and *Strix* (König and Weick 2008). Polymorphism in owls has been most-studied in the Eastern Screech-Owl (*Megascops asio*), Tawny Owl (*Strix aluco*), and Barn Owl (*Tyto alba*).

The existence of distinct rufous and gray color-morphs of the Eastern Screech-Owl (Fig. 1) has long intrigued ornithologists. The rufous phenotype appears to be controlled by a dominant allele and gray by its recessive form, but the existence of intermediate-colored birds suggests a multiple allelic system (Gehlbach 1994, 1995). Owen (1963a) found that the variation in this species is bimodal (i.e., intermediates are uncommon) and that the relative frequency of the two color-morphs varies geographically throughout the species' range. The range-wide pattern shows a high percentage of rufous birds (70–80%) in the center of the range, decreasing to 20–30% rufous birds, or even lower (0–20%; Marshall 1967, Gehlbach 1994) at the periphery of the range (Hasbrouck 1893, Owen 1963a, Johnsgard 1988).

In many polymorphic species, differently colored individuals are not randomly distributed among environments and they often have different physiological attributes, reproductive parameters, and behavioral and life-history traits (Roulin 2004). Thus, the evolution and maintenance of genetic color polymorphism may be based on a balance of selection pressures that enables the morphs to exploit alternative ecological niches (Fisher 1930). However, the adaptive significance of polymorphism is poorly understood. Climatic factors (temperature and humidity) have been thought to select for one color versus another in the Eastern Screech-Owl for over a century (Hasbrouck 1893, Gehlbach 1994). Mosher and

[1]Department of Biology, Luther College, Decorah, IA 52101, USA; e-mail: sordahlt@luther.edu

FIG. 1. Rufous and gray color-morphs of the Eastern Screech-Owl (*Megascops asio*). Original watercolor painting by Dana Gardner, based on study skins of Iowa screech-owls in the Hoslett Museum of Natural History at Luther College.

Henny (1976), in an experimental study, identified a physiological mechanism for the influence of climate on the distribution of color-morphs in screech-owls. They showed that rufous birds have higher mass-specific oxygen requirements at low environmental temperatures than gray birds. This appears to be because of pleiotropic effects linking metabolism and plumage color (Ducrest et al. 2008), but different thermal properties of the feather colors could also play a role (Dexter 1996). Greater metabolic requirements could select against rufous birds during hard winters and at the northern part of the species' range, as well as in any low-quality environment where food is difficult to obtain.

Polymorphism appears to enhance crypsis in specific habitats. Screech-owls with rufous feathers seem better camouflaged in the dim light and vegetation associated with cloudy weather in humid climates (Gehlbach 1994, Duncan 2003). The common occurrence of color-morphs in predators suggests that apostatic (frequency-dependent) selection may be important in maintaining polymorphism by effectively making each morph rarer; thus the visual characteristics of both morphs are less familiar to their prey (and to their own predators as well), making search image formation more difficult (Mather 1955, Paulson 1973, Caro 2005). By enhancing crypsis or otherwise reducing intraspecific aggression, polymorphism may also enable subordinate individuals of a species to exist as "floaters" in the territories of more dominant conspecifics (Galeotti and Cesaris 1996).

Gray feather coloration is caused by the deposition of eumelanin in the feather cortex and rufous feather coloration is caused by deposition of phaeomelanin (Hill 2010, Pannkuk et al. 2010). Melanin may make feathers more resistant to wear in environments that are brushy, dry and dusty, or exposed to high solar UV radiation (Burtt 1979, Bonser 1995, McGraw 2006; but see Pannkuk et al. 2010), and more resistant to feather-degrading bacteria, which are more abundant in humid environments (Burtt and Ichida 2004, Goldstein et al. 2004, Shawkey and Hill 2004, McGraw 2006). Color variation in birds has also been associated with behavioral syndromes (Ducrest et al. 2008), including variation in the adrenocortical stress response (Horton and Holberton 2010), aggressive behavior (Ficken et al. 1978), gonad size (Murton et al. 1973), reproductive strategy (Lank et al. 1995, Roulin et al. 2003), and resistance to ectoparasites (Roulin et al. 2001).

In summary, ecological factors like temperature, humidity, vegetation type, solar radiation, predation, parasitism, and social behavior affect the survival and reproduction of screech-owls. They may operate differentially on the color-morphs by mechanisms like differential metabolism, crypsis, apostatic selection, feather strength and thermal properties, and possibly hormonal response, immunocompetence, and reproductive strategy. Thus these factors are likely to influence the relative geographic distribution of rufous and gray morph screech-owls.

Although the Eastern Screech-Owl is a textbook example of clinal variation in color-morph ratio (Gill 2007), the pattern is known only at a very coarse scale (Owen 1963a). In this paper, I examine the distribution of color-morphs of Eastern Screech-Owls in Iowa, which lies in the northwestern part of the species' range (Fig. 2). I show, at a finer scale than has previously been attempted, that there is a clinal geographic pattern in the morph ratio. In addition to the relationship between plumage color and geographic location, I also investigate variation in the morph ratio by sex, climate, and over time.

METHODS

I collected records of color-morphs of Eastern Screech-Owls in Iowa from four sources (Table 1): (1) Museum specimens—I sent questionnaires to Iowa colleges and universities ($n = 40$) and to major U.S. museums ($n = 12$), requesting data on museum specimens in their care; (2) Wildlife rehabilitation records—I sent questionnaires to zoos ($n = 3$) and wildlife rehabilitation centers ($n = 7$) in Iowa and neighboring states; (3) Bird-banding records—I wrote to bird-banders active in banding raptors in Iowa ($n = 4$); (4) Sight records—I obtained sight records from bird watchers by personal contacts, by advertising in the Iowa Ornithologists' Union's newsletter and the state's largest newspaper (*Des Moines Register*), and by limited field work using playback to attract owls close enough to observe their color. Minimum data required were the county, date, and plumage category. For museum specimen, bird-banding, and wildlife rehabilitation records, reporters were asked to place the bird in one of three plumage categories (i.e., rufous, intermediate, gray). For sight records, reporters were asked to indicate whether the bird was rufous or gray. For

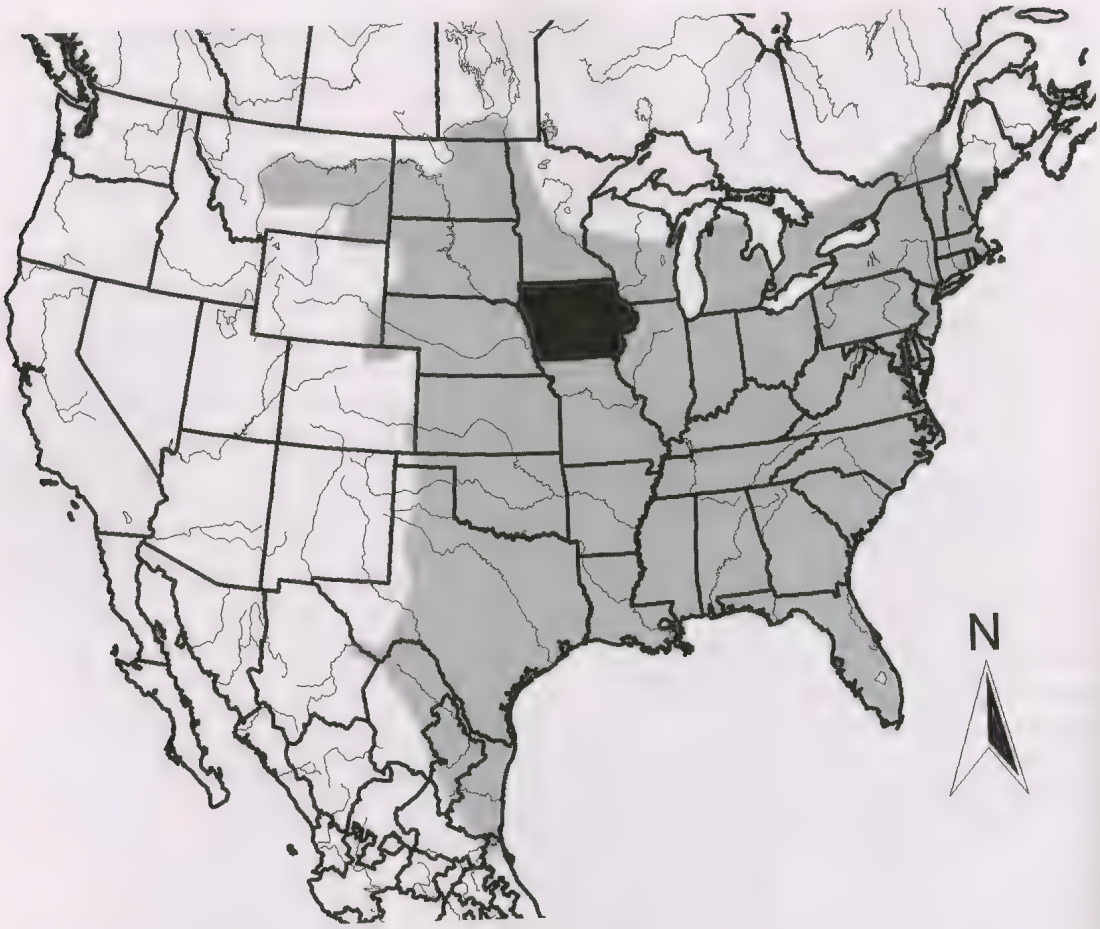


FIG. 2. Geographic range of the Eastern Screech-Owl in the United States (Gehlbach 1995), showing the location of Iowa in black.

museum specimens, the sex and collector also were requested. Observers were instructed to avoid reporting the same owl more than once, and I examined all records to avoid potential pseudoreplication of data. Color differences between morphs are so pronounced that assigning an individual owl to its morph category is easy and accurate.

TABLE 1. Number of records of Eastern Screech-Owl color-morphs collected from Iowa.

Type of record	Color-morph category			Totals
	Rufous	Intermediate	Gray	
Museum specimen	68	9	44	121
Wildlife rehabilitation	40	1	68	109
Bird-banding	54	5	73	132
Sight	51	2	104	157
Totals	213	17	289	519

Iowa's 99 counties are fairly uniform in size and are laid out in columns and rows. To test whether the relative frequency of rufous screech-owls shows a west-east or north-south geographic pattern in Iowa, I first divided the state into the nine regions used by the Iowa Department of Agriculture and the state climatologist (following Kent and Dinsmore 1996). I used the nine regions to divide the state into western, central, and eastern bands and into northern, central, and southern tiers. I used heterogeneity chi-square analyses (Zar 1999) to determine whether the four types of records gathered in this study (Table 1) could be pooled. A 3 (region) X 2 (color) chi-square test of independence was used to determine if the regions differed in the relative frequency of rufous birds, and adjusted standardized residuals were calculated to determine specifically which regions differed from the others (Runyon et al. 2000).

TABLE 2. Number of records of Eastern Screech-Owl color-morphs from 68 of Iowa's 99 counties.

County	Color-morph category			Totals
	Rufous	Intermediate	Gray	
Allamakee	6	1	3	10
Audubon	0	0	1	1
Benton	1	0	3	4
Black Hawk	3	0	16	19
Boone	5	2	10	17
Bremer	1	0	0	1
Buchanan	2	0	0	2
Buena Vista	1	0	0	1
Calhoun	1	0	0	1
Carroll	1	0	1	2
Cedar	3	0	2	5
Cerro Gordo	3	1	11	15
Cherokee	0	0	1	1
Chickasaw	0	0	1	1
Clarke	3	0	14	17
Clay	0	1	4	5
Clayton	13	0	2	15
Clinton	0	0	1	1
Crawford	0	1	3	4
Davis	1	0	1	2
Decatur	1	0	4	5
Delaware	1	1	1	3
Des Moines	1	0	0	1
Dickinson	4	0	3	7
Fayette	2	0	2	4
Franklin	1	0	1	2
Fremont	0	0	1	1
Greene	1	0	0	1
Grundy	1	0	1	2
Hamilton	0	0	1	1
Hancock	2	0	1	3
Henry	1	0	1	2
Ida	1	0	2	3
Iowa	1	0	1	2
Jasper	0	0	1	1
Jefferson	1	0	0	1
Johnson	18	2	10	30
Jones	3	0	1	4
Kossuth	1	0	8	9
Lee	2	0	1	3
Linn	15	1	6	22
Louisa	1	0	0	1
Lucas	1	0	3	4
Madison	2	0	2	4
Mahaska	0	0	1	1
Marion	15	3	22	40
Marshall	6	0	4	10
Mills	1	0	0	1
Monona	0	0	2	2
Muscatine	2	0	1	3
O'Brien	2	0	2	4
Palo Alto	2	0	0	2
Pocahontas	1	0	10	11
Polk	4	1	11	16
Pottawattamie	1	0	1	2
Ringgold	0	0	2	2
Sac	4	0	10	14
Scott	30	0	41	71
Shelby	0	0	1	1
Story	8	1	7	16
Union	7	0	1	8
Wapello	0	0	1	1
Warren	0	0	4	4
Washington	3	0	3	6
Webster	0	0	1	1
Winneshiek	21	2	36	59
Woodbury	0	0	3	3
Worth	1	0	0	1
Totals	213	17	289	519

To further test for geographic patterns in the percentage of rufous screech-owls, I obtained the latitude and longitude for each of Iowa's counties and conducted regression analyses with those counties having 10 or more records, using the nonparametric Spearman's correlation coefficient (Snedecor and Cochran 1967). To test whether the percentage of rufous screech-owls changed over time, I conducted a similar regression analysis with those decades (beginning with pre-1900) having 10 or more records. I used the Agresti-Coull method for estimating confidence intervals of proportions to calculate 95% confidence intervals for the samples in each decade (Whitlock and Schluter 2009). Because the early decades had few records, I also divided the span of records into six 20-year periods, and used a 6×2 chi-square test to determine if plumage color was independent of time. I used a 2×2 chi-square test to determine if plumage color was independent of sex. Statistical tests were conducted by hand or with SPSS (SPSS 2010), and significance was set at an α level of 0.05.

RESULTS

A total of 519 records were collected for the entire state (Table 1), representing 68 of Iowa's 99 counties (Table 2), and spanning the time period 1880–2003. There were 213 (41.0%) records of rufous birds, 289 (55.7%) records of gray birds, and 17 (3.3%) records of intermediate birds. In the museum specimen subsample, where intermediates could be determined accurately, the

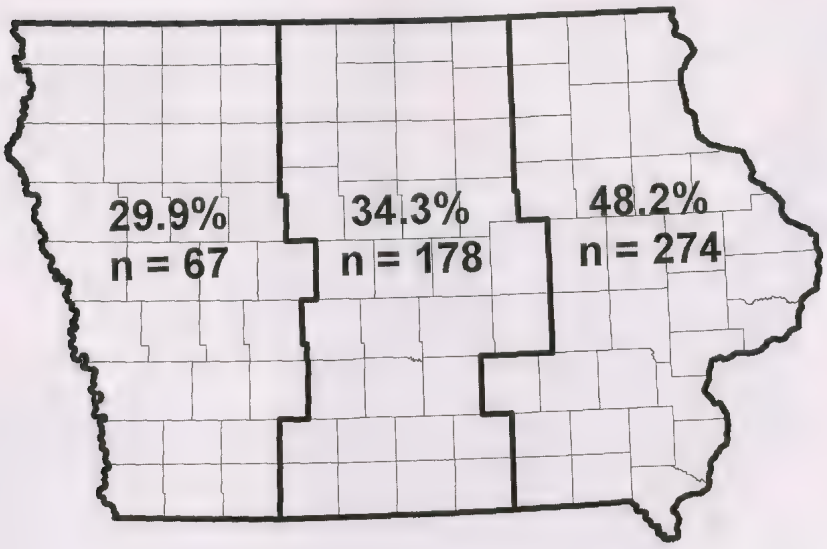


FIG. 3. Percentage of rufous color-morph records of the Eastern Screech-Owl from western, central, and eastern Iowa. Differences between the three regions are statistically significant in all comparisons (see text).

frequency of intermediates was 7.4%. Because the number of intermediate-plumaged Eastern Screech-Owls is small, I combined them with gray birds and consider only two categories, rufous and non-rufous, in my analyses (following Owen 1963a).

For all records in which the sex of the bird was reported, 21 of 47 males (44.7%) were rufous and 34 of 59 females (57.6%) were rufous. The difference was not statistically significant (χ^2 = 1.76, df = 1, P = 0.185). In the museum specimen subsample, where sex was presumably identified more accurately by dissection, the results were similar; 14 of 32 males (43.8%) were rufous and 31 of 52 females (59.6%) were rufous. The difference was not statistically significant (χ^2 = 2.00, df = 1, P = 0.157).

The percentage of rufous screech-owls increased clinally from the western to central to eastern thirds of Iowa (Fig. 3). Heterogeneity chi-square analysis indicated that museum specimen, wildlife rehabilitation, bird-banding, and sight record samples could be combined (χ^2 = 6.84, df = 6, P = 0.351). A chi-square 3 × 2 test of independence on the combined samples showed a significant difference between western, central, and eastern regions in the relative frequency of rufous morphs (χ^2 = 12.60, df = 2, P = 0.002). Adjusted standardized residuals were calculated for each cell and revealed that the relative frequency of rufous morphs differs significantly in all comparisons between western, central, and eastern regions. In a similar test, the four sample groups were combined (heterogeneity χ^2 = 3.33, df = 6, P = 0.764), and the relative frequency of rufous screech-owls did not differ between the northern, central, and southern tiers of Iowa (Fig. 4; χ^2 = 1.72, df = 2, P = 0.422). The adjusted standardized residuals revealed no significant differences in comparisons between northern, central, and southern regions.

For the 16 counties with at least 10 color-morph records, the percentage of rufous screech-owls correlated negatively with longitude (Fig. 5; r_s = −0.68, P = 0.004, n = 16). However, the percentage of rufous screech-owls did not correlate with latitude (Fig. 6; r_s= 0.02, P = 0.935, n = 16).

For the eight decades with at least 10 color-morph records, the percentage of rufous screech-owls correlated negatively with time (Fig. 7; r_s = −0.86, P = 0.006, n = 8). Combining the decades into six 20-year periods also indicated a significant difference between time periods in the relative frequency of rufous morphs (χ^2 = 33.58, df = 5, P < 0.001).

DISCUSSION

Overall Color-morph Ratio.—The composite sample of 519 screech-owl color-morph records collected in this study yielded 41.0% rufous birds and 59.0% non-rufous birds (55.7% gray and

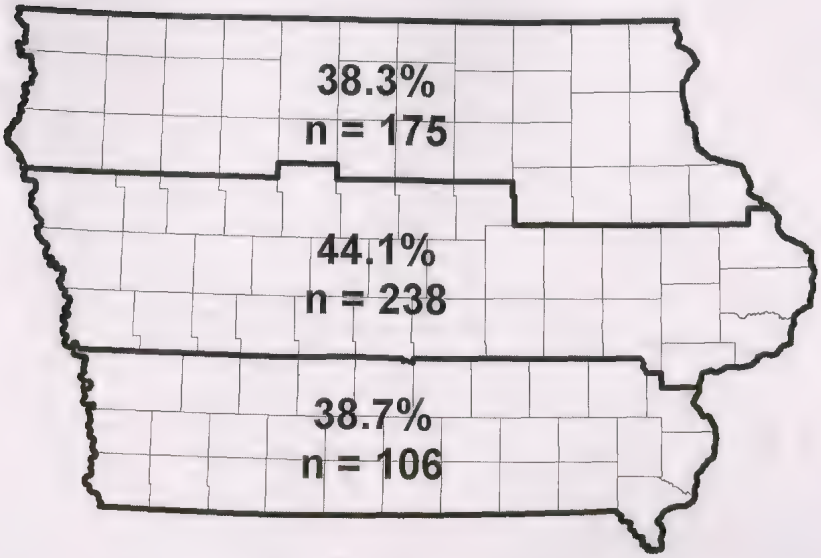


FIG. 4. Percentage of rufous color-morph records of the Eastern Screech-Owl from northern, central, and southern Iowa. Differences between the three regions are statistically nonsignificant (see text).

3.3% intermediate). Owen (1963a) presented two data points in or near Iowa that suggest a percentage of rufous birds between 33–57% for the state. Schorger (1954) reported 38.7% (n = 235) rufous screech-owls in a sample of road-killed birds in southern Wisconsin and northern Illinois over a 19-year study. Over the entire species' range, Owen (1963a) found 38% rufous and 8% intermediate birds in a sample of 1,320 specimens. Gehlbach (1995) reported 36% rufous owls range-wide.

Sexual Differences in Color-morph Frequency.—Color polymorphism is often referred to as being "independent" of sex, age, and season,

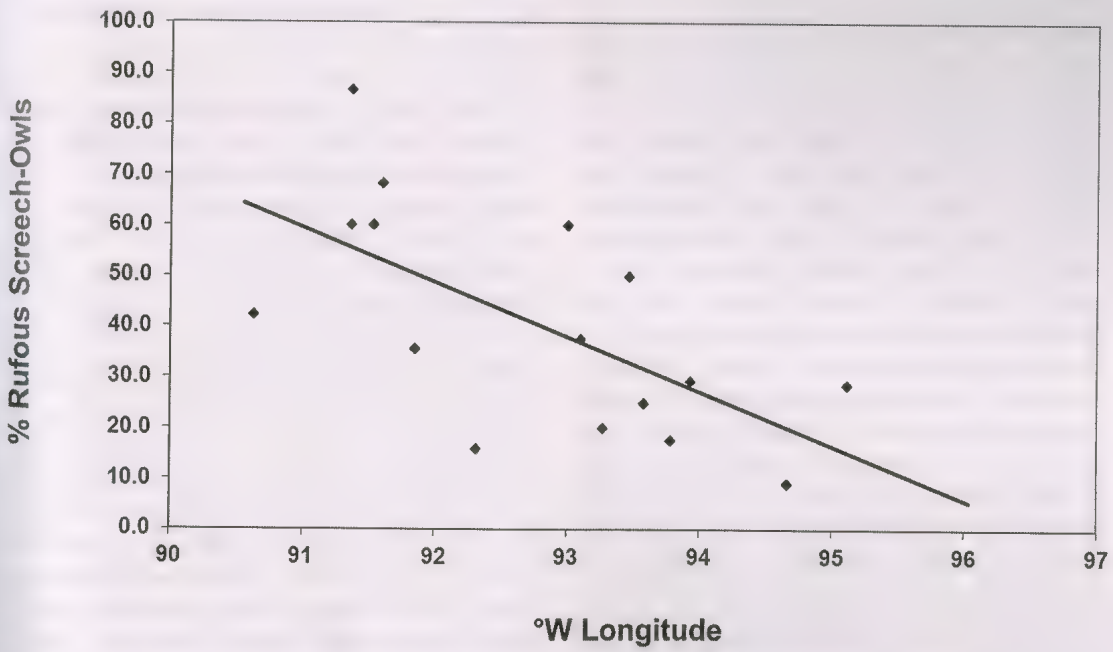


FIG. 5. Percentage of rufous color-morph records of the Eastern Screech-Owl plotted against longitude for the 16 Iowa counties with at least 10 records. Sum of squares best fit line is shown. $r_s = -0.68$, $P = 0.004$.

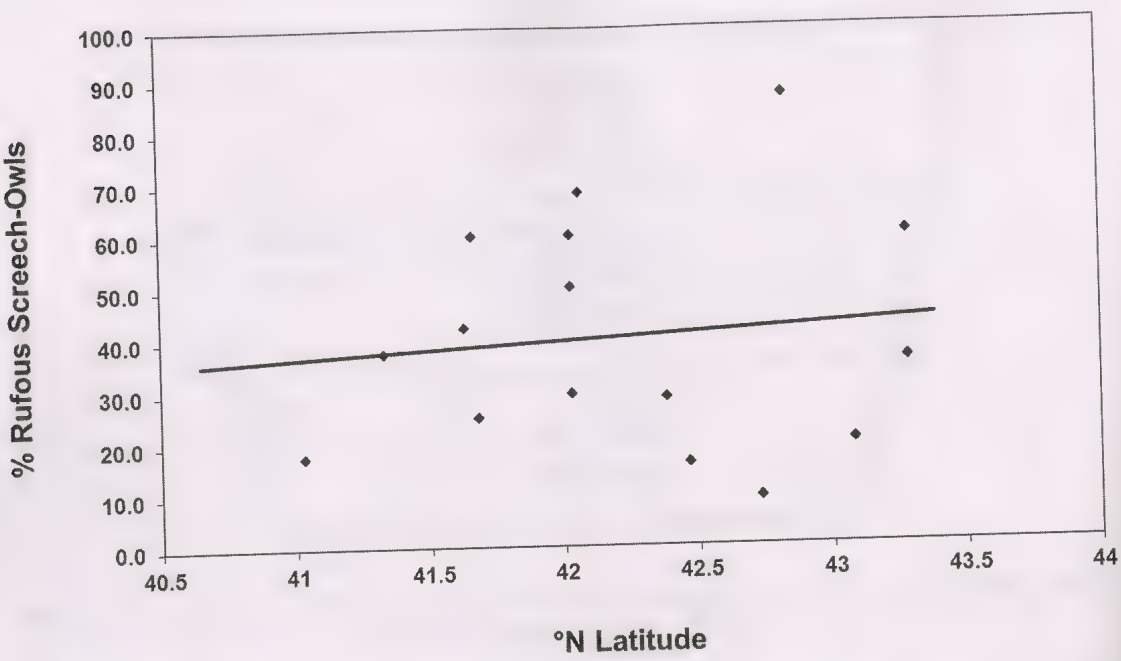


FIG. 6. Percentage of rufous color-morph records of the Eastern Screech-Owl plotted against latitude for the 16 Iowa counties with at least 10 records. Sum of squares best fit line is shown. $r_s = 0.02$, $P = 0.935$.

meaning that all morphs occur in both sexes and morph type does not change with age or time of year. I found that 44.7% of male screech-owls and 57.6% of females were rufous. Hasbrouck (1893) reported that 33.7% of 276 males and 80.3% of 370 females were rufous across the species' range; the difference was statistically significant ($\chi^2 = 143.3$, df = 1, $n = 646$, $P < 0.001$). Gehlbach (1994) reviewed the topic of sex differences in morph ratios and found evidence that more females than males are rufous (Gehlbach 1994 for central Texas, Hasbrouck 1893 for species' range, but not by VanCamp and Henny 1975 for northern Ohio). Although my results were not statistically significant, their trend is consistent with the conclusion that female Eastern Screech-Owls are more likely to be rufous than are males. If factors like low temperature, high humidity, and feather wear select for gray plumage, then males may be more exposed to that selection than females. Female screech-owls are larger than males and perform all incubation and brooding in a sheltered nest cavity (Gehlbach 1995), so they may experience less selection for gray plumage by cold, UV radiation, or feather abrasion. Also, pleiotropic effects often associated with dark color in vertebrates, such as greater aggressiveness and sexual activity (Ducrest et al. 2008), may benefit males more than females.

Morph Ratio and Climate.—My data show a significant west to east cline of increasing rufous in the morph ratio across Iowa, both when analyzed by region and by regression against longitude. There was no north to south pattern in the morph ratio. Climate data for Iowa show an average annual temperature range from 46 °F (7.8 °C) in the north to 52 °F (11.1 °C) in the southeast, average annual precipitation range from 25 inches (63.5 cm) per year in the northwest to 34 inches (86.4 cm) in the southeast, and 20 inches (50.8 cm) of snow per year in the southeast to 40 inches (101.6 cm) in the northeast (Garoogian 2000). The pattern of mean annual precipitation across Iowa shows a longitudinal increase from west to east, whereas the mean annual temperature pattern shows an increase from north to south (Corcoran and Johnson 2005). This suggests that the morph ratio distribution of Eastern Screech-Owls in Iowa is more strongly influenced by precipitation than by temperature.

Morph Ratios and Subspecies.—Six subspecies of Eastern Screech-Owl were recognized by Gehlbach (2003). Two of those subspecies, the western *M. a. maxwelliae* and the eastern *M. a. naevius* (sometimes included in *M. a. asio*; Marshall 1967, Gehlbach 1995), occur in Iowa. Their ranges overlap along a north-south intergrade

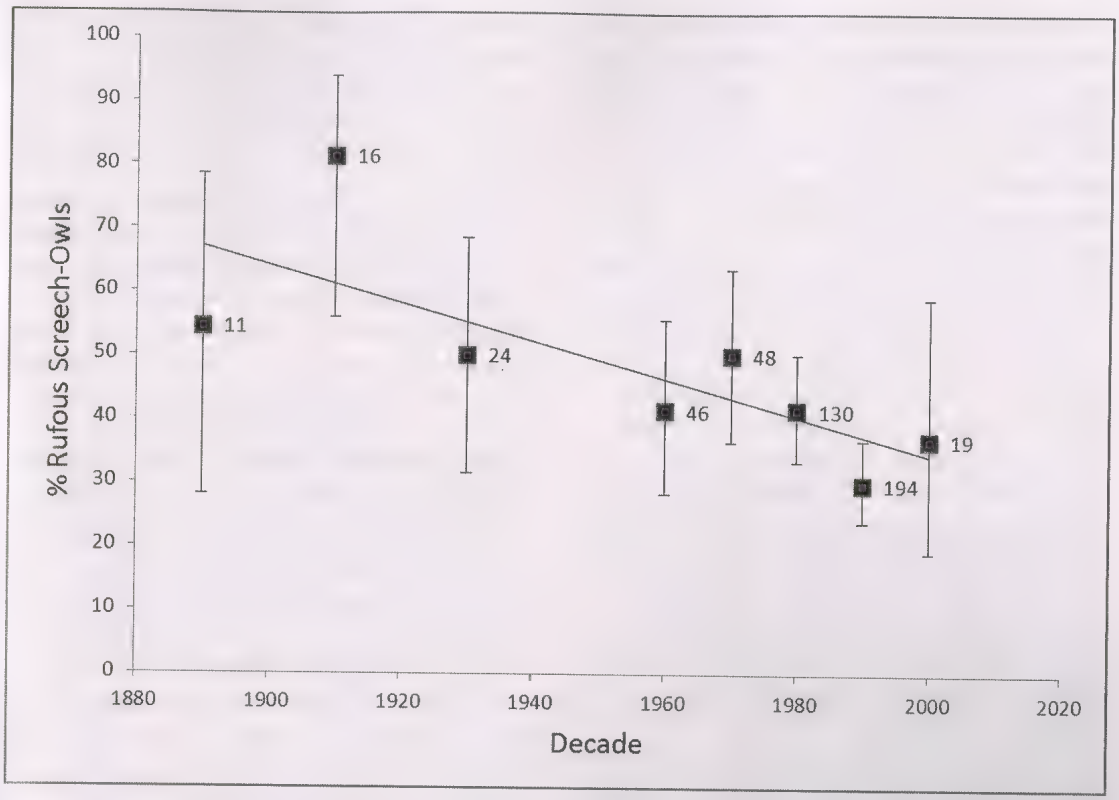


FIG. 7. Percentage of rufous color-morph records of the Eastern Screech-Owl plotted against time for the eight decades with at least 10 records. Sample size and 95% confidence interval are given for each point. Sum of squares best fit line is shown. $r_s = -0.86$, $P = 0.006$.

zone about one-third of the way across the state from its western border. The western form (*maxwelliae*) may have a lower ratio of rufous morphs than the eastern form (*naevius/asio*), as indicated by Marshall (1967). However, Marshall (1967) also noted that most subspecific variation is continuous. The broad-scale results of Owen (1963a) show considerable variation in morph ratios across the range of each subspecies, indicating that individual subspecies are not characterized by particular morph ratios. Owen's (1963b) overall analysis of morphological variation in the Eastern Screech-Owl led him to reject the subspecies concept because of smooth clinal variation. Proudfoot et al. (2007) also found little evidence for recognizing subspecies based on variation in mitochondrial DNA. My finer-scale data show clinal variation in morph ratio, with no apparent abrupt changes. Therefore, although the existence of two subspecies and their intergrade zone in Iowa could produce the morph ratio pattern of my data, the evidence is equivocal for that interpretation.

Changes in Morph Ratio Over Time.—In balanced polymorphism, such as the Eastern Screech-Owl exhibits, a balance of selection pressures prevents one morph from replacing the other (Fisher 1930, Huxley 1955). The morph ratio changes geographically because environmental conditions change. Environmental conditions also change through time, so morph ratios can be expected to track those changes. My results, for records dating 1880–2003, indicate that the morph ratio in Iowa changed over periods of 10 and 20 years. Although the sample size is small for older records, it appears that rufous morphs were more common in early decades than in later ones (Fig. 7).

My data show a temporal trend in morph ratio, but the sample sizes are too small and the scale too coarse to resolve multiple changes that may have occurred over time. Short-term changes in weather, food supply, or predators can cause relatively rapid changes in morph ratio. VanCamp and Henny (1975) observed dramatic changes in morph ratio from 9.3–26.8% rufous over a 30-

year study in northern Ohio. They attributed the changes to higher mortality of rufous birds during hard winters. Gehlbach (1994) found a temporal relationship between rufous plumage and both mild winters and increased precipitation. He attributed those relationships to the rufous morph being poorly adapted to cold and more cryptic in rainy and cloudy weather.

Ecological Aspects of Polymorphism.—Although plumage polymorphisms can be selectively neutral (Bortolotti 2006), this seems unlikely for the Eastern Screech-Owl, given that it is known to exhibit morph-specific differences in survival under specific environmental conditions. In a comprehensive comparative survey of polymorphism in birds, Galeotti et al. (2003) found that polymorphic species tend to be active during both day and night and tend to occupy multiple or semi-open habitats. Both conditions apply to Eastern Screech-Owls. Galeotti et al. (2003) concluded that these patterns suggest that plumage polymorphism evolved under selection pressures related to bird detectability, as affected by variable backgrounds.

The main geographical trend in my data is a west to east increase in the percentage of rufous birds. Most screech-owls in Iowa live in small woodlands, shelterbelts, farmsteads, and towns (Jackson et al. 1996, Kent and Dinsmore 1996). The Mississippi River forms the eastern border of the state and eastern Iowa has numerous riparian corridors that may provide habitat with reduced light, where rufous birds are thought to be more cryptic (Gehlbach 1995). Moving westward across Iowa, habitats become drier and more open, with fewer trees, conditions in which gray birds might be more cryptic.

The species-wide pattern of the color-morph ratio in Eastern Screech-Owls has been challenging for investigators to explain. It appears that multiple factors influence the morph ratio and will be required to explain the pattern. At the core of the species' range, where environmental conditions may be optimal (Brown 1984, Brown et al. 1995), rufous morphs predominate. Rufous appears to be caused in a proximate sense by a dominant allele. In an ultimate sense, rufous may be favored over gray by better camouflage and lower metabolic requirements in the center of the range (Mosher and Henny 1976, Gehlbach 1994). Dexter (1996) found that gray morphs have lower metabolic rates and both darker feathers and darker skin on their dorsal surface (which would facilitate absorption of solar radiation) than rufous morphs. He concluded that rufous owls are adapted for energy-rich environments where food is readily available, whereas gray owls are adapted for relatively low-quality, energy-poor environments.

The morph ratio variation in Eastern Screech-Owls seems to fit a model where rufous morphs are better-adapted at the center of the range, but gray morphs are selected for at the periphery. At the northern part of the range cold weather may select for gray over rufous (Mosher and Henny 1976). In the southern part of the range the environment is humid, which promotes the action of feather-degrading bacteria. In the western part of the range, environments are more open and less humid, with greater exposure to UV radiation and wind-blown particles. If eumelanin confers greater resistance to feather-degrading bacteria and abrasion than phaeomelanin, then these environmental factors may select for gray feathers at the southern and western periphery of the species' range. However, the relative performance of melanin subtypes is unknown, and the total melanin concentration of rufous versus gray screech-owls is also unknown. In the first experimental study attempting to determine if melanin subtype could lead to differential strength in biological tissues, Pannkuk et al. (2010) found no difference in the strength variables they measured between rufous and gray contour feathers of Eastern Screech-Owls. This result challenges hypotheses for the maintenance of morph ratio variation that seem to depend on feather strength differences, such as feather abrasion, feather-degrading bacteria, and UV radiation.

Ecogeographical mapping of morph frequency and determination of ratio clines, if present, is a first step in the analysis of polymorphism (Huxley 1955). For Eastern Screech-Owls, this has been accomplished in broad scale by Owen (1963a). However, larger sample sizes and finer-scale mapping, as in this study, may enable new insights into the dynamics of polymorphism. A second step in analyzing polymorphisms is the evaluation of the selective advantages of each morph (Huxley 1955). Studies are needed of micro-habitat selection by roosting and hunting screech-owls. The camouflage value of rufous versus gray plumage in different habitats remains conjectural. Because screech-owls hunt at night, visual camouflage may be important primarily in

daytime roosting by concealing the birds from their predators and mobbers. The demonstration that Eastern Screech-Owl color-morphs differ in metabolic rate (Mosher and Henny 1976, Dexter 1996) was a significant advance toward understanding their geographic distribution. More studies of thermal properties and durability of Eastern Screech-Owl feathers, including comparisons of melanin subtypes, would enable better evaluation of some of the hypotheses discussed above for ratio clines in screech-owl color-morphs.

ACKNOWLEDGMENTS

I thank all of the people who provided records of screech-owl color-morphs. Museum specimen records were obtained from the following collections (curators): Bert H. Bailey Museum, Coe College (H. Hadow); Buena Vista University Collection (S. F. Lehtinen); Burke Museum, University of Washington (S. A. Rohwer); Central College Natural History Collection (H. P. Whidden); Cornell College Collection (D. Lyon); Field Museum of Natural History (P. E. Lowther); Iowa State University Collection (J. J. Dinsmore); Mt. Mercy College Collection (N. P. Bernstein); National Museum of Natural History (J. P. Angle); Putnam Museum Collection (S. D. Hinz); Sherman A. Hoslett Museum of Natural History, Luther College (T. A. Sordahl); University of Iowa Museum of Natural History (G. D. Schrimper); University of Michigan Museum of Zoology (R. B. Payne); University of Nebraska State Museum (P. W. Freeman); University of Northern Iowa Museum (J. M. Trainer). Wildlife rehabilitators who submitted records were: B. L. Brown, J. Cancilla, B. Ehresman, R. Harms, K. Neumann. Bird-banders who submitted records were: D. W. De Geus, B. Ehresman, P. C. Petersen. Observers who reported sight records were: R. E. Betts, K. Cakerice, D. Carter, C. E. Curl, S. J. Dinsmore, S. Etringer, T. Etringer, C. Fisher, I. J. Frisbie, T. Gedler, J. Gilliam, R. Goranson, D. Halbmaier, R. Harms, D. Koenig, K. Lawless, F. Lesher, B. Linge, K. Mason, C. Moritz, E. Munson, M. Olson, D. Poggensee, C. L. Rector, M. J. Schmeiser, D. Sedivec, G. Sickels, D. Smith, T. A. Sordahl, L. Stone, J. Stravers, E. Thelen, D. Webber, H. P. Whidden, and H. Zaletel.

I am grateful to C. L. Liggett for help with data analysis and to S. L. Stevenson for assistance with various aspects of manuscript preparation. E. Baack, D. I. Bishop, and J. W. Eckblad contributed statistical advice. K. J. Larsen prepared Figures 2–4. G. Ritchison and two anonymous reviewers made helpful comments on the manuscript. I especially thank Dana Gardner for the watercolor painting (Fig. 1).

LITERATURE CITED

Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. Condor 97:590–591.

Bortolotti, G. R. 2006. Natural selection and coloration: protection, concealment, advertisement, or deception? Pages 3–35 *in* Bird coloration. Volume 2. Function and evolution (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, Cambridge, Massachusetts, USA.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124:255–279.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028–2043.

Burtt Jr., E. H. 1979. Tips on wings and other things. Pages 75–123 *in* The behavioral significance of color (E. H. Burtt Jr., Editor). Garland STPM Press, New York, USA.

Burtt Jr., E. H. and J. M. Ichida. 2004. Gloger's rule, feather-degrading bacteria, and color variation among Song Sparrows. Condor 106:681–686.

Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois, USA.

Corcoran, W. T. and E. Johnson. 2005. Climate of North America. Pages 525–534 *in* Encyclopedia of world climatology (J. E. Oliver, Editor). Springer, Dordrecht, The Netherlands.

del Hoyo, J., A. Elliott, and J. Sargatal (Editors). 1994. Order Falconiformes. Pages 23–275 *in* Handbook of the birds of the world. Volume 2. New World vultures to guineafowl. Lynx Edicions, Barcelona, Spain.

Dexter, M. A. 1996. Plumage dichromatism and thermal ecology of the Eastern Screech-Owl (*Otus asio*). Thesis. Wake Forest University, Winston-Salem, North Carolina, USA.

Ducrest, A.-L., L. Keller, and A. Roulin. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. Trends in Ecology and Evolution 23:502–510.

Duncan, J. R. 2003. Owls of the world: their lives, behavior and survival. Firefly Books, Buffalo, New York, USA.

Ficken, R. W., M. S. Ficken, and J. P. Hailman. 1978. Differential aggression in genetically different morphs of the White-throated Sparrow (*Zonotrichia albicollis*). Zeitschrift für Tierpsychologie 46:43–57.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, England.

Galeotti, P. and C. Cesaris. 1996. Rufous and grey colour morphs in the Italian Tawny Owl: geographical and environmental influences. Journal of Avian Biology 27:15–20.

Galeotti, P., D. Rubolini, P. O. Dunn, and M. Fasola. 2003. Colour polymorphism in birds: causes and functions. Journal of Evolutionary Biology 16:635–646.

Garoogian, D. (Editor). 2000. Weather America: a thirty-year summary of statistical weather data and rankings. Second Edition. Grey House Publishing, Millerton, New York, USA.

Gehlbach, F. R. 1994. The Eastern Screech-Owl: life history, ecology, and behavior in the suburbs and countryside. Texas A & M University Press, College Station, USA.

GEHLBACH, F. R. 1995. Eastern Screech-Owl (*Otus asio*). The birds of North America. Number 165.

GEHLBACH, F. R. 2003. Body size variation and evolutionary ecology of Eastern and Western screech-owls. Southwestern Naturalist 48:70–80.

GILL, F. B. 2007. Ornithology. Third Edition. W. H. Freeman, New York, USA.

GOLDSTEIN, G., K. R. FLORY, B. A. BROWNE, S. MAJID, J. M. ICHIDA, AND E. H. BURTT JR. 2004. Bacterial degradation of black and white feathers. Auk 121:656–659.

HANCOCK, J. AND J. KUSHLAN. 1984. The herons handbook. Harper and Row, New York, USA.

HASBROUCK, E. M. 1893. Evolution and dichromatism in the genus *Megascops*. American Naturalist 27:521–533, 638–649.

HILL, G. E. 2010. National Geographic bird coloration. National Geographic Society, Washington, D.C., USA.

HORTON, B. M. AND R. L. HOLBERTON. 2010. Morph-specific variation in baseline corticosterone and the adrenocortical response in breeding White-throated Sparrows (*Zonotrichia albicollis*). Auk 127:540–548.

HUXLEY, J. 1955. Morphism in birds. International Ornithological Congress 11:309–328.

JACKSON, L. S., C. A. THOMPSON, J. J. DINSMORE, B. L. EHRESMAN, J. FLECKENSTEIN, R. CECIL, L. M. HEMESATH, AND S. J. DINSMORE. 1996. The Iowa breeding bird atlas. University of Iowa Press, Iowa City, USA.

JOHNSGARD, P. A. 1988. North American owls: biology and natural history. Smithsonian Institution Press, Washington, D.C., USA.

KENT, T. H. AND J. J. DINSMORE. 1996. Birds in Iowa. Published by the authors, Iowa City and Ames, Iowa, USA.

KÖNIG, C. AND F. WEICK. 2008. Owls of the world. Second Edition. Yale University Press, New Haven, Connecticut, USA.

LANK, D. B., C. M. SMITH, O. HANOTTE, T. BURKE, AND F. COOKE. 1995. Genetic polymorphism for alternative mating behaviour in lekking male Ruff *Philomachus pugnax*. Nature 378:59–62.

MARSHALL JR., J. T. 1967. Parallel variation in North and Middle American screech-owls. Monographs of the Western Foundation of Vertebrate Zoology, Number 1.

MATHER, K. 1955. Polymorphism as an outcome of disruptive selection. Evolution 9:52–61.

MAYR, E. 1970. Populations, species, and evolution. Harvard University Press, Cambridge, Massachusetts, USA.

MCGRAW, K. J. 2006. Mechanics of melanin-based coloration. Pages 243–294 *in* Bird coloration. Volume 1. Mechanisms and measurements (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, Cambridge, Massachusetts, USA.

MOSHER, J. A. AND C. J. HENNY. 1976. Thermal adaptiveness of plumage color in screech owls. Auk 93:614–619.

MURTON, R. K., N. J. WESTWOOD, AND R. J. P. THEARLE. 1973. Polymorphism and the evolution of a continuous breeding season in the pigeon, *Columba livia*. Journal of Reproduction and Fertility, Supplement 19, 561–575.

OWEN, D. F. 1963a. Polymorphism in the screech owl in eastern North America. Wilson Bulletin 75:183–190.

OWEN, D. F. 1963b. Variation in North American screech-owls and the subspecies concept. Systematic Zoology 12:8–14.

PANNKUK, E. L., L. M. SIEFFERMAN, AND J. A. BUTTS. 2010. Colour phases of the eastern screech owl: a comparison of biomechanical variables of body contour feathers. Functional Ecology 24:347–353.

PAULSON, D. R. 1973. Predator polymorphism and apostatic selection. Evolution 27:269–277.

PROUDFOOT, G. A., F. R. GEHLBACH, AND R. L. HONEYCUTT. 2007. Mitochondrial DNA variation and phylogeography of the Eastern and Western screech-owls. Condor 109:617–627.

ROULIN, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. Biological Reviews 79:815–848.

ROULIN, A., B. DUCRET, P.-A. RAVUSSIN, AND R. ALTWEGG. 2003. Female colour polymorphism covaries with reproductive strategies in the Tawny Owl *Strix aluco*. Journal of Avian Biology 34:393–401.

ROULIN, A., C. RIOLS, C. DIJKSTRA, AND A.-L. DUCREST. 2001. Female plumage spottiness signals parasite resistance in the Barn Owl (*Tyto alba*). Behavioral Ecology 12:103–110.

RUNYON, R. P., K. A. COLEMAN, AND D. J. PITTENGER. 2000. Fundamentals of behavioral statistics. Ninth Edition. McGraw-Hill, New York, USA.

SCHORGER, A. W. 1954. Color phases of the screech owl between Madison, Wisconsin, and Freeport, Illinois. Auk 71:205.

SHAWKEY, M. D. AND G. E. HILL. 2004. Feathers at a fine scale. Auk 121:652–655.

SIBLEY, D. A. 2000. The Sibley guide to birds. Alfred A. Knopf, New York, USA.

SNEDECOR, G. W. AND W. G. COCHRAN. 1967. Statistical methods. Sixth Edition. Iowa State University Press, Ames, USA.

SPSS. 2010. SPSS for Windows, Version 19.0. SPSS, Inc., Chicago, Illinois, USA.

VANCAMP, L. F. AND C. J. HENNY. 1975. The screech owl: its life history and population ecology in northern Ohio. North American Fauna Number 71.

WHITLOCK, M. C. AND D. SCHLUTER. 2009. The analysis of biological data. Roberts and Company, Greenwood Village, Colorado, USA.

ZAR, J. H. 1999. Biostatistical analysis. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Short Communications

The Wilson Journal of Ornithology 126(2):333–338, 2014

Snow Buntings Sing Individually Distinctive Songs and Show Inter-annual Variation in Song Structure

Sarah Baldo,[1,4] Daniel J. Mennill,[1,4] Sarah Guindre-Parker,[1,3] H. Grant Gilchrist,[2] and Oliver P. Love[1]

ABSTRACT.—Birds use song to communicate with conspecifics, and song can influence both intra-sexual competition and inter-sexual mate choice. Some birds produce repertoires consisting of hundreds of songs while others produce a single song type. For species with a single-song repertoire, there are varying levels of inter-individual variation which can be the result of environmental, genetic, and physiological factors. Male Snow Buntings (*Plectrophenax nivalis*) typically produce a single song type, and while syllable sharing occurs between individuals, many researchers have anecdotally noted the individuality of each male's song. To investigate this long-held assertion, we performed a detailed bioacoustic analysis of male Snow Buntings recorded in the Canadian Arctic. We use canonical discriminant analysis to provide quantitative evidence confirming that male Snow Buntings sing individually distinctive songs. Furthermore, we present the first evidence that some Snow Buntings exhibit inter-annual variation in song structure; while songs remain consistent within each year, two males changed their song type between years. Inter-individual variation in song content can have important behavioral implications, because it facilitates individual recognition and can affect individual fitness. *Received 26 September 2013. Accepted 20 January 2014.*

Key words: individual distinctiveness, individual recognition, inter-annual variation, *Plectrophenax nivalis*, Snow Bunting, song.

Birds rely heavily on acoustic communication to facilitate survival and reproduction. Songs are generally long, complex vocalizations that birds use for territory defense and mate attraction (Tinbergen 1939, Catchpole and Slater 2008). In some bird species, each individual produces a repertoire of songs comprised of multiple song types (e.g., *Parus major*; McGregor et al. 1982) although the most common song repertoire size is one (e.g., *Poecile atricapillus*; Horn et al. 1992; MacDougall-Shackleton 1998). In species with a single song type repertoire, there can still be tremendous variation between individuals, where individuals of some species sing nearly identical songs and individuals of other species sing remarkably different songs (Catchpole and Slater 2008).

Snow Buntings (*Plectrophenax nivalis*) are Arctic-breeding passerines which use song for mate attraction and territory defense (Tinbergen 1939, Nethersole-Thompson 1966). Although syllable sharing occurs, each male sings a single song type which has been qualitatively described as individualistic (Tinbergen 1939, Borror 1961, Drury 1961, Nethersole-Thompson 1966, Montgomerie and Lyon 2011). The only quantitative study to date (Espmark 1995) showed higher coefficients of variation in song features between males compared to within males, supporting the idea of individual distinctiveness. In this study, we conducted a detailed bioacoustic analysis of field recordings and used discriminant analysis to determine whether or not individuals could be quantitatively distinguished based on fine structural features of their song. We also recorded birds that returned to the study site across multiple years to describe inter-annual variation. Individual distinctiveness in songs has been demonstrated in other songbird species and can have important inter-sexual and intra-sexual implications.

METHODS

Song Recording and Analysis.—We recorded 19 male Snow Buntings on East Bay (Mitivik) Island, Nunavut, Canada in June and July 2010 and 2011. East Bay Island is covered with loose granite rock which provides ideal nesting habitat

[1] Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada.
[2] Environment Canada, National Wildlife Research Centre, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1A 0H3, Canada.
[3] Current address: Department of Ecology, Evolution, and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York City, NY 10027, USA.
[4] Corresponding authors; e-mail: baldos@uwindsor.ca and dmennill@uwindsor.ca

for Snow Buntings and is likely responsible for the high breeding densities on the island (Guindre-Parker et al. 2013). We used a directional microphone (Sennheiser K6/ME66) and a solid-state digital recorder (Marantz PMD 660; 44,100 Hz sampling rate, 16 bit accuracy, WAVE format). All of the recorded birds were distinguished by unique color band combinations as part of a long-term monitoring project (see Guindre-Parker et al. 2013). In the laboratory, we filtered recordings to remove background noise outside the song range of Snow Buntings (high-pass frequency: 867 Hz; low-pass frequency: 13,939 Hz) and normalized recordings to −3 dB in Audition v. 3.0 (Adobe, San Jose, CA, USA). We then performed detailed measurements of time and frequency features in Avisoft SAS Lab Pro v. 5.2 (R. Sprecht, Berlin, Germany) using the automated parameter measurement tool (temporal resolution: 5.8 ms; frequency resolution: 86 Hz); this approach minimized human measurement error and subjectivity. Syllable counts and syllable typing were determined by visual inspection. We defined ''syllables'' as elements or clusters of elements that fell into clear groupings, and syllables that looked different from one another were considered to be different types.

We analyzed 10 songs from each male (following from Espmark 1995, 1999; Hofstad et al. 2002), focusing on high quality songs with minimal overlapping non-target sounds. The 10 songs were taken from multiple sessions on different days for each individual (mean ± SE: 2.68 ± 0.22 recording days/individual; range: 2–5 days). For each individual, the recording sessions were collected on days that ranged from 1–13 days apart (mean ± SE: 6.05 ± 0.77 days between sessions). For four males, we collected fewer than 10 high quality songs in our focal recordings; for these males we included 1–7 songs recorded by an array of autonomous digital recorders placed across the island (Wildlife Acoustics SM2-GPS; 22,050 Hz sampling rate, 16 bit accuracy, WAVE format; details in Mennill et al. 2012). We ensured these recordings unambiguously originated from the same males as the focal recordings by assessing both the location of the recording and the spectral similarity of the song.

We measured the following structural features from 190 songs: (1) song length (time from start to end of a song, in sec); (2) note duration (sum of note lengths within a song, in sec; equivalent to duty cycle); (3) total number of syllables; (4) number of unique syllable types; (5) minimum song frequency; (6) maximum song frequency; (7) average minimum syllable frequency (average across all syllables in each song); and (8) average maximum syllable frequency (average across all syllables in each song). All frequency measurements were calculated relative to a threshold of −30 dB below the maximum in AviSoft.

Statistical Analysis.—We conducted a canonical discriminant function analysis to test whether songs could be correctly assigned to the birds that produced them. We ran the discriminant analysis using a cross-validation approach. We randomly selected 75% of the data (i.e., we randomly selected 75% of the data across all males, so that each of the 19 males contributed 6 to 9 songs to the initial stage of analysis) and performed the discriminant analysis on these data. We then tested the accuracy of the discriminant analysis on the remaining 25% of the data (i.e., 1–4 songs from each of the 19 males).

RESULTS

Songs sung by different male Snow Buntings were readily distinguished when viewed as spectrograms by an analyst (Fig. 1). Discriminant analysis of measurements of the fine structural details of songs confirmed that males sing individually-distinctive songs: cross-validation assigned 91.5% of songs to the correct male (41 out of 44 songs in the cross validation dataset), significantly higher than the 5.3% expected by chance for 19 males (i.e., a chance rate of one in 19; binomial test, $P < 0.001$; Fig. 2). Variables that contributed most strongly to the first canonical axis were *average minimum syllable frequency* and *average maximum syllable frequency*, and this axis explained 32% of the variation in males' songs. Variables that contributed most strongly to the second canonical axis were *number of unique syllable types* and *average maximum syllable frequency*, and this axis explained 27% of the variation in males' songs. The 95% confidence ellipse for each male overlapped with the 95% confidence ellipses of 6.1 ± 0.6 other males in the plot of the first canonical versus second canonical axes (Fig. 2), indicating that most males can be distinguished from each other on the basis of just these two canonical axes.

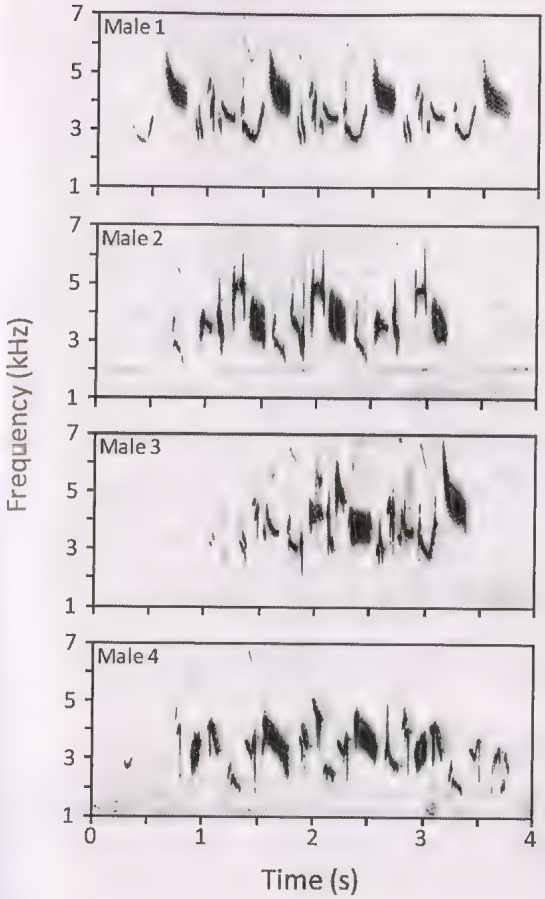


FIG. 1. Sound spectrograms of four example songs of male Snow Buntings recorded on East Bay Island, Nunavut. Songs were analyzed with an automated parameter measurement tool and individual distinctiveness was confirmed with a canonical discriminant analysis. These four songs were chosen to represent typical songs within our study population.

We recorded three males in both 2010 and 2011. We discovered that while most male Snow Buntings produce a single song type within each breeding season, there is inter-annual variation in song structure. Two of the three males we recorded in both 2010 and 2011 sang songs in 2011 which showed striking differences from the previous year (Fig. 3). These birds were neighbors in 2011 and produced songs that were similar to one another in that year.

DISCUSSION

We provide quantitative evidence confirming the long-held assertion that male Snow Buntings sing songs that are individually distinctive. This song feature of Snow Buntings has been reported anecdotally since the 1930s, based on observations from locations around the world including Scotland, Norway, Greenland, and Canada (Tinbergen 1939, Borror 1961, Drury 1961, Nethersole-Thompson 1966, Espmark 1995, Montgomerie and Lyon 2011). A study of Snow Buntings in Norway revealed significant differences between individuals in song features, and higher coefficients of variation in acoustic features between individuals compared to within individuals (Espmark 1995). We used bioacoustic measurements of songs, including songs from the same males sampled repeatedly on different days, followed by discriminant analysis to demonstrate that songs could be assigned to the correct individuals at levels that exceed chance. The average minimum and maximum syllable frequencies, as well as the number of unique syllable types, were the most important features in these discriminant analyses, suggesting that these may be the most distinctive components of a Snow Bunting's song. Our results are the first to show inter-annual variation in the song structure of Snow Buntings; two of three banded males that were recorded in two separate years sang different songs, whereas one male maintained the same song across years.

Within a species, song often shows significant inter-individual variation. This variation can provide important information to conspecifics, including individual identity. Being able to distinguish between individuals may be beneficial for multiple reasons. For example, individual recognition can play a role in territory defense, with individuals recognizing and habituating to familiar neighbors, decreasing the costs of territory defense against established territorial rivals (Brooks and Falls 1975). Further, female songbirds may discriminate between different males' songs which can have important reproductive implications (Lind et al. 1996, Wiley et al. 2010). Snow Buntings are socially monogamous but genetically promiscuous (Espmark and Moksnes, unpubl. data cited in Hofstad et al. 2002), and individually distinctive songs may allow females to distinguish between social partners and extra-pair partners, for example. Snow Buntings nest within rock crevices, and song recognition may be particularly important for cavity-nesting species since it can facilitate effective intra-pair communication in the absence of visual cues (Lind et al. 1996). This is in line with Nethersole-Thompson's (1966) suggestion

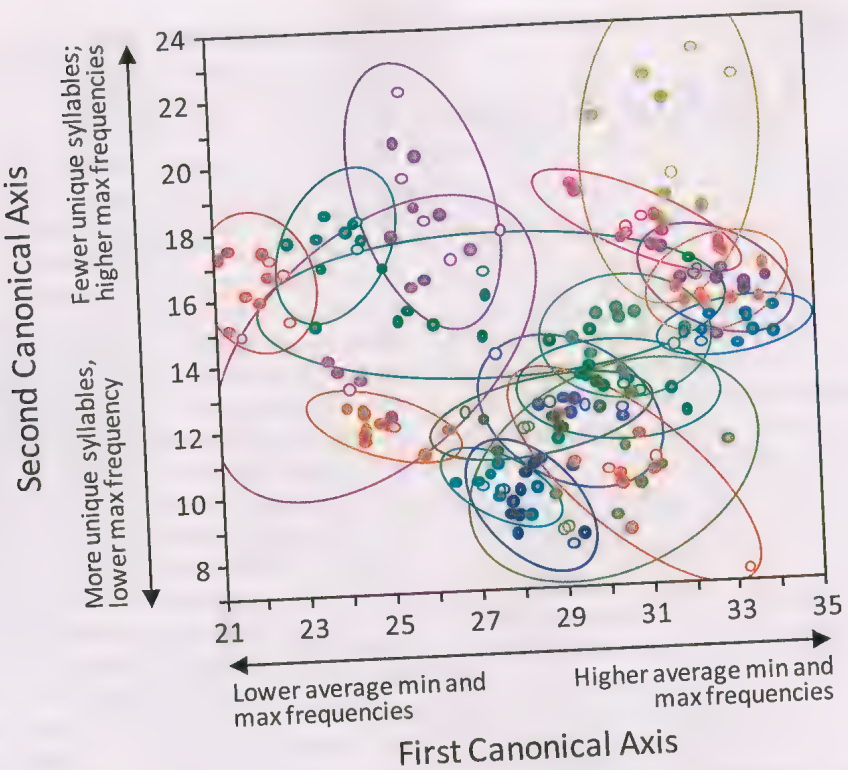


FIG. 2. Plot of the first two canonical axes from discriminant analysis between 19 Snow Buntings on the basis of eight fine structural measurements of males' songs. Each of the 19 males is represented by a different color, and all 10 songs are shown for each male, including the sounds used to construct the discriminant analyses (filled circles) and those used in cross-validation (open circles). 95% confidence ellipses around the multivariate mean for each male are shown.

that males may use song to call brooding females off their nests. Additionally, individual recognition may be important for parent-offspring contact; fledged Snow Bunting chicks seemingly recognize and respond to their father's song (Nethersole-Thompson 1966; SB, pers. obs.).

To the best of our knowledge, inter-annual variation in song structure has never been reported in Snow Buntings. We recorded three birds in 2010 and 2011 and found that two of them changed their song between years. Interestingly, in 2011 two of these individuals were neighbors and produced similar songs to one another (Fig. 2). There are two suggested processes behind song sharing: instructive learning and selective-based learning (Nelson and Marler 1994). Instructive learning suggests that song sharing results from birds learning the local dialect or song(s) of their neighbors as young birds or upon settling on new territories. Selective learning suggests birds learn a variety of song types and then retain and produce a subset of songs that best match neighbors' songs or the local dialect (Nelson and Marler 1994). We suggest that males may learn a variety of syllables, or full songs, and hone in on one song type at the start of each year, possibly to match the songs of nearby local males. This is in line with the observation that neighbors' songs were occasionally nearly identical, with high syllable sharing, on Svalbard (Espmark 1999), and that local dialects occurred in Greenland (Tinbergen 1939) and the Canadian Arctic (Montgomerie and Lyon 2011). White-crowned Sparrows (*Zonotrichia leucophrys*), like most Snow Buntings, produce a single song type as adults, but often over-produce multiple songs at the start of their first breeding season before selecting one song (Hough et al. 2000). A similar process may occur annually in Snow Buntings.

At least three areas are important for future research on Snow Bunting song: (1) Although we have demonstrated that songs contain individually distinctive features, playback studies will be required to confirm that Snow Buntings use this information to distinguish between individuals, possibly using neighbor-stranger discrimination experiments (as in Brooks and Falls 1975, for

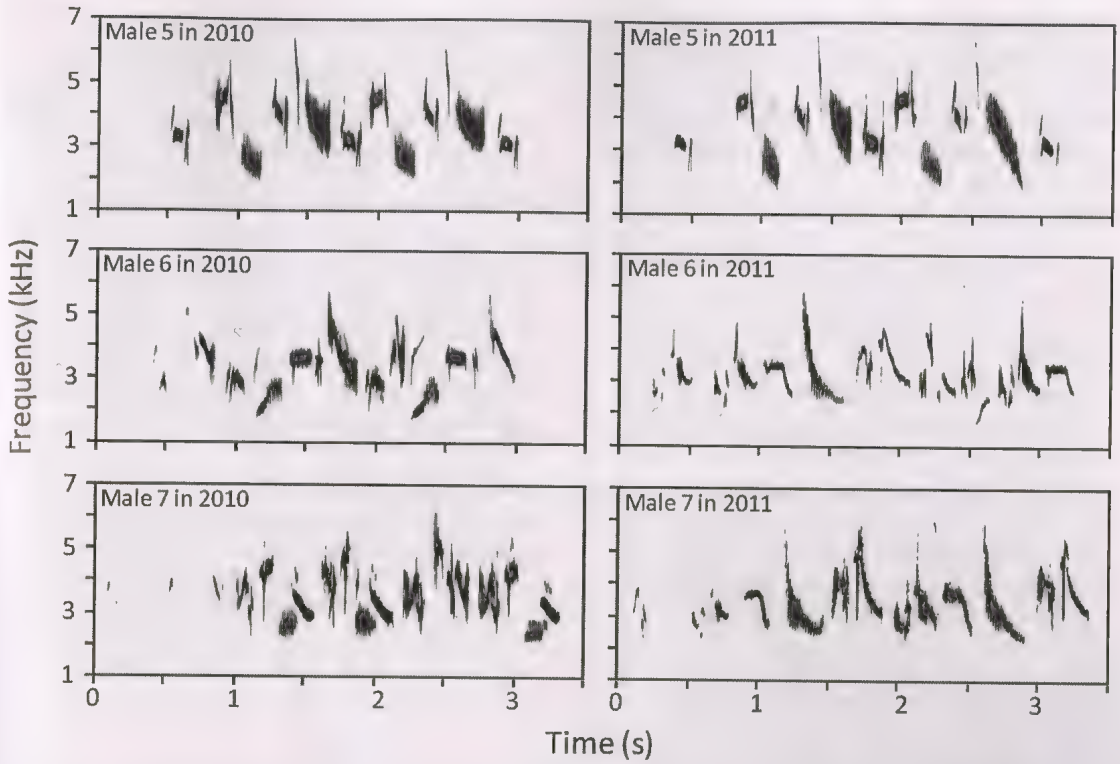


FIG. 3. Within a breeding season, a male Snow Bunting sings a single individually distinctive song. However, between-year recordings of three color-banded males reveal that two males (Male 6 and Male 7) showed inter-annual variation in song structure.

example). (2) Tinbergen (1939) studied Snow Buntings in Greenland and noted that neighbors' songs can sometimes sound nearly identical. In 2011, we encountered a pair of neighboring males singing highly similar songs (Male 6 and 7; Fig. 3), although our discriminant analysis confused the males in these pairs rarely (only 1 of 20 songs was misclassified as the neighbor). Further studies should investigate how often adjacent territorial males produce similar songs and whether this phenomenon has social consequences for territorial dynamics. (3) Longitudinal studies should be performed to further examine the similarity of a male's song across years. Future studies that follow the same individuals over multiple years may further our understanding of the factors affecting song learning, the proximate role of song in Snow Buntings, and the degree of intra-male song flexibility in this species.

ACKNOWLEDGMENTS

For field support we thank the researchers at East Bay Island. For financial support we thank the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, Environment Canada, the Polar Continental Shelf Project, Aboriginal Affairs and Northern Development Canada, the Government of Ontario, and the University of Windsor.

LITERATURE CITED

BORROR, D. J. 1961. Songs of finches (Fringillidae) of eastern North America. Journal of Science 61:161–174.

BROOKS, R. J. AND J. B. FALLS. 1975. Individual recognition by song in White-throated Sparrows. I. Discrimination of songs of neighbors and strangers. Canadian Journal of Zoology 53:879–888.

CATCHPOLE, C. K. AND P. J. B. SLATER. 2008. Bird song: biological themes and variations. Cambridge University Press, Cambridge, UK.

DRURY, W. H. 1961. Studies of the breeding biology of Horned Lark, Water Pipit, Lapland Longspur, and Snow Bunting on Bylot Island, Northwest Territories, Canada. Bird-Banding 32:1–46.

ESPMARK, Y. 1995. Individual and local variations in the song of the Snow Bunting (*Plectrophenax nivalis*) on Spitsbergen. Bioacoustics 6:117–133.

ESPMARK, Y. 1999. Song of the Snow Bunting (*Plectrophenax nivalis*) in areas with and without sympatric passerines. Canadian Journal of Zoology 77:1385–1392.

GUINDRE-PARKER, S., H. G., GILCHRIST, S. BALDO, S. M. DOUCET, AND O. P. LOVE. 2013. Complex signaling

with simple plumage: multiple ornaments in an achromatic species. Behavioural Ecology 24:672–682.

HOFSTAD, E., Y. ESPMARK, A. MOKSNES, T. HAUGAN, AND M. INGEBRIGTSEN. 2002. The relationship between song performance and male quality in Snow Buntings (*Plectrophenax nivalis*). Canadian Journal of Zoology 80:524–531.

HORN, A. G., M. L. LEONARD, L. RATCLIFFE, S. A. SHACKLETON, AND R. G. WEISMAN. 1992. Frequency variation in songs of Black-capped Chickadees (*Parus atricapillus*). Auk 109:847–852.

HOUGH, G. E., D. A. NELSON, AND S. F. VOLMAN. 2000. Re-expression of songs deleted during vocal development in White-crowned Sparrows *Zonotrichia leucophrys*. Animal Behaviour 60:279–287.

LIND, H., T. DABELSTEEN, AND P. K. MCGREGOR. 1996. Female Great Tits can identify mates by song. Animal Behaviour 52:667–671.

MACDOUGALL-SHACKLETON, S. A. 1998. Sexual selection and the evolution of song repertoires. Current Ornithology 14:81–125.

MCGREGOR, P. K., J. R. KREBS, AND C. M. PERRINS. 1982. Song repertoires and lifetime reproductive success in the Great Tit (*Parus major*). American Naturalist 118:149–159.

MENNILL, D. J., M. BATTISTON, D. R. WILSON, J. R. FOOTE, AND S. M. DOUCET. 2012. Field test of an affordable, portable wireless microphone array for spatial monitoring of animal behaviour. Methods in Ecology and Evolution 3:704–712.

MONTGOMERIE, R. AND B. LYON. 2011. Snow Bunting (*Plectrophenax nivalis*). The birds of North America. Number 198.

NELSON, D. A. AND P. MARLER. 1994. Selection-based learning in bird song development. Proceedings of the National Academy of Sciences of the United States of America 91:10498–10501.

NETHERSOLE-THOMPSON, D. 1966. The Snow Bunting. Oliver and Boyd, Edinburgh, Scotland.

TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. Transactions of the Linnean Society, New York, USA.

WILEY, R. H., B. J. HATCHWELL, AND N. B. DAVIES. 2010. Recognition of individual males' songs by female Dunnocks: a mechanism increasing the number of copulatory partners and reproductive success. Ethology 88:145–153.

The Wilson Journal of Ornithology 126(2):338–345, 2014

Hybridization of a Lesser Black-backed Gull and Herring Gulls in Eastern North America

Julie C. Ellis,[1,5] Steven M. Bogdanowicz,[2] Mary Caswell Stoddard,[3] and L. William Clark[4]

ABSTRACT.—We present the first confirmed case of hybridization between a Lesser Black-backed Gull (*Larus fuscus*) and Herring Gulls (*Larus argentatus*) in North America (outside of Greenland). We discovered a Lesser Black-backed Gull × Herring Gull pair on Appledore Island, Maine in 2007. Nuclear DNA analysis indicated that the Lesser Black-backed Gull was the genetic parent of the chicks from 2008 to 2011. The offspring have not returned to breed, so we do not know if they are fertile. Increasing numbers of observations of Lesser Black-backed Gulls, including putative Lesser Black-backed Gull × Herring Gull hybrids along the Atlantic coast, indicate that Lesser Black-backed Gulls may be in the process of colonizing North America. If so, additional hybridization with Herring Gulls is likely in areas of overlap. *Received 11 June 2013. Accepted 13 February 2014.*

Key words: avian hybridization, Gulf of Maine, large white-headed gulls, *Larus argentatus*, *Larus fuscus*, range expansion.

Lesser Black-backed Gulls (*Larus fuscus*, Linnaeus, 1758) breed primarily in northern and western Europe and have undergone a significant range expansion north and west as well as south during the past century (Cramp and Simmons 1983, Calladine 2004, Boertmann 2008). The species colonized Iceland between 1920–1930 and Greenland between 1986–1990. They also colonized the Netherlands, Germany, Spain, Portugal, and recently expanded to the Canary Islands (Cramp and Simmons 1983, Grande and Palacios 2002). This expansion mainly involved the subspecies *graellsii* (Post and Lewis 1995).

[1] Department of Infectious Disease and Global Health, 200 Westboro Road, Cummings School of Veterinary Medicine at Tufts University, North Grafton, MA 01536 USA.

[2] Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853-2701, USA.

[3] Harvard University, Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, MA 02138, USA.

[4] P. O. Box 71, Kresgeville, PA, 18333, USA.

[5] Corresponding author; e-mail: julie.ellis@tufts.edu

The first record of Lesser Black-backed Gulls in North America (outside of Greenland) was in coastal New Jersey in 1934 (Edwards 1935). Records of this species in North America increased slowly from 1950 to the mid-1970s, with substantial increases thereafter. By 1994, Lesser Black-backed Gulls had been reported in all 31 states in the eastern half of the United States except for West Virginia (Post and Lewis 1995, Olsen and Larsson 2004). Particularly large concentrations (33% of all Lesser Black-backed Gulls found during annual winter counts 1996–2006) have been found in Pennsylvania (Hallgrimsson et al. 2011). Significant numbers have also been reported in Florida, New Jersey, Virginia and North Carolina (Rutt 2009). Most observations of Lesser Black-backed Gulls along the Atlantic coast of North America occur from September–May, but increasingly the species is observed June–August (Fogarty 2009). There is virtually no information on the origins of Lesser Black-backed Gulls in America. Only two firm records of banded Lesser Black-backed Gulls exist: a bird banded in Iceland that was resighted in Puerto Rico in 2002 and a bird banded in the Netherlands that was resighted in Cold Spring Harbor, New York in 1997 (Hallgrimsson et al. 2011).

In spite of increasing numbers of birds overwintering in eastern North America, no breeding had been observed. The one previous observation of breeding by a Lesser Black-backed Gull in North America was in 1993 (van Vliet et al. 1993) wherein a Lesser Black-backed Gull was observed near a Herring Gull (*Larus argentatus*, Pontoppidan 1763) sitting on a nest containing two eggs near Juneau, Alaska. The nesting attempt was apparently unsuccessful; the authors returned to the site on 25 July 1993 and found eggshell fragments near the nest along with both members of the pair. However, there was no evidence of juveniles at or near the nest.

Herring Gulls breed inland across Canada and Alaska and along the coasts of Alaska, the Great Lakes, and northeastern and mid-Atlantic U.S. (Pierotti and Good 1994). The species increased dramatically during the 20th century, leading to a southward range expansion along the Atlantic coast (Pierotti and Good 1994). However, in the past decade, numbers appear to have declined in the northeast U.S. (Welch et al. 2010). Recent genetic evidence indicates that the American Herring Gull is differentiated from the European Herring Gull (*L. argentatus*) and that the two taxa are not each other's closest relatives (Liebers et al. 2004, Sternkopf et al. 2011). Hybridization between Lesser Black-backed Gulls and European Herring Gulls has been described (Tinbergen 1953, Harris et al. 1978), but the only record of potential hybridization between a Lesser Black-backed Gull and American Herring Gull is the observation by vanVliet et al. (1993).

We discovered a Lesser Black-backed Gull × Herring Gull pair on Appledore Island, Maine, in 2007 (Ellis et al. 2008). The individual was banded in 2008 and returned to breed on the island every year since, except 2012, when it did not appear on the island. Here we provide three lines of evidence (genetic, behavioral, phenotypic) that strongly suggest that the Lesser Black-backed Gull produced hybrid offspring with more than one Herring Gull.

METHODS

Study Site

A Lesser Black-backed Gull × Herring Gull pair was observed on Appledore Island, Maine (42° 59′ N, 70° 36′ W), in the Isles of Shoals. The Isles of Shoals is a nine-island archipelago located approximately 10 km from the coast of New Hampshire. Appledore Island is the site of a large, mixed-species colony of Great Black-backed Gulls (*Larus marinus*, Linnaeus, 1758) and Herring Gulls. In 2009, there were approximately 660 pairs of Herring Gulls and 539 pairs of Great Black-backed Gulls on the island (JCE, unpubl. data). A Lesser Black-backed Gull was observed on Appledore Island once prior to our study; this bird was seen on 11 September 2006 near the same location where it nested in 2007 (S. Mirick, pers. comm.).

Breeding Chronology and Banding

We first discovered the pair at a nest with two eggs in May 2007 on the southeast portion of the island (Ellis et al. 2008). The nest was located on a bare rock ledge in a sub-colony of Herring Gulls and was within ~1 m of the same location each year from 2008–2011. Adult gulls were captured for banding during incubation with a walk-in nest trap; chicks were caught by hand from the nesting territory. All birds were banded with one metal band (provided by the Bird Banding Laboratory, USGS) and one plastic field readable band. A website and blog were established to facilitate resights of banded birds by the public.

TABLE 1. Summary of genetic sampling conducted from 2007–2011. Samples are identified by the code on the field readable leg band placed on each bird. In 2010, the chick died and was not banded.

Sample ID	Identity	Year sampled	Source of DNA
F02, F03	Chick	2008	Feather pulp
F05	Lesser Black-backed Gull	2007, 2008	Feather pulp
F04, F06	Chick	2009	Blood
Dead chick (unbanded)	Chick	2010	Tissue
F07	Chick	2011	Blood
K75	Herring Gull	2011	Blood

In 2007, the pair produced two eggs and successfully fledged one chick, which was banded. In 2008, we banded the Lesser Black-backed Gull and Herring Gull mate, monitored the nest for offspring, and banded the chick. Each year from 2009–2012, we noted the presence of the Lesser Black-backed Gull, recorded the identity of the Herring Gull mate (as indicated by the leg band), recorded the number of eggs and chicks, and banded pre-fledgling chicks.

Tissue Sampling for Genetic Analyses

We collected feathers or blood from the Lesser Black-backed Gull, one of the Herring Gull mates, and all chicks except one that died before hatching (tissue was collected from this chick). DNA obtained from the Lesser Black-backed Gull and Herring Gull mate was used to confirm sex and for paternity analyses. DNA from the chicks was used in paternity analyses. In order to place the genotypic data in a broader context, we also obtained feather pulps from Herring Gulls across Appledore in 2004 that were part of long-term population studies (JCE, unpubl. data). None of the individual birds used in that study were known to be genetically related; in a few cases, both members of a mated pair were sampled. Blood was taken from a brachial vein; feather pulp was obtained by plucking a growing feather from a bird. The samples were stored in an EDTA–DMSO–NaCl buffer (Seutin et al. 1991). We sampled a total of 66 Herring Gulls (65 from across Appledore and one from 2011 that appeared to be the mate of the LBBG). Genomic DNA was extracted from feather pulps with a DNeasy tissue kit (Qiagen, Valencia, CA). DNA from the male Lesser Black-backed Gull (LBBG) was extracted from a feather collected from the nest (2007) and from plucked feathers (2008) (Table 1). DNA from the Herring Gull associated with the male LBBG in 2011 was extracted from a blood sample; this is the only year that both putative parents were sampled. DNA from presumably hybrid chicks was extracted from feathers, blood, and tissue from live or dead chicks (Table 1).

Genetic Analyses

Isolation of Microsatellite Loci, Primer Design, and Genotyping.—Microsatellite loci were isolated from libraries constructed separately for each gull species. We followed the protocol described by Hamilton (1999) and Pincus et al. (1999) with some modifications (Appendix 1). PCR primers flanking microsatellite repeats were designed by the program PRIMERSELECT (Lasergene, Madison, WI). Primers, dyes, and PCR fragment size of the clone are shown in Table 2; additional methodological details regarding primers can be found in supplemental material.

TABLE 2. Microsatellite locus name, primer sequences and 5′ dyes, and PCR fragment size predicted from the cloned sequence. La and Lm indicate loci isolated from *L. argentatus* and *L. marinus* libraries, respectively.

Locus	Dye	Forward Primer (5′-3′)	Reverse Primer (5′-3′)	Fragment size (bp, clone)
La5	NED	gtcccaccaatccccactg	atcctaactgcaaatgtatcaccta	132
Lm7	VIC	tctgggaggtgcacaagggaata	gggggagaataaatggacaataata	259
Lm13	PET	ccaccaatccccactgagta	tccccttatagtttttcctcctc	260
Lm17	VIC	gcagggcttgtttgaggtct	gcctgctaatgctttgttgtga	171
Lm23	NED	ggactctggccctggaaca	agaagcctaacccaaaaagtaacct	202
Lm25	6FAM	ccatgggagtcacctgcttac	agtagatcagtttgtttggctttt	148

TABLE 3. Allele sizes and (frequencies) for six microsatellite loci genotyped from 65 Herring Gulls collected from Appledore Island, Maine in 2004.

La5ned	Lm7fam	Lm13pet	Lm17vic	Lm23ned	Lm25fam
134 (0.180328)	254 (0.3221)	265 (0.169)	172 (0.040)	192 (0.164)	157 (0.033)
136 (0.811475)	258 (0.139)	267 (0.822)	182 (0.774)	194 (0.057)	159 (0.016)
145 (0.008197)	260 (0.121)	275 (0.008)	184 (0.064)	195 (0.197)	161 (0.240)
	262 (0.322)		186 (0.073)	197 (0.115)	164 (0.198)
	266 (0.078)		190 (0.040)	204 (0.303)	165 (0.041)
	270 (0.017)		192 (0.008)	205 (0.049)	168 (0.215)
				206 (0.016)	170 (0.016)
				210 (0.016)	172 (0.066)
				211 (0.033)	174 (0.107)
				212 (0.049)	176 (0.033)
					180 (0.016)
					191 (0.008)
					193 (0.008)

Sex Determination.—We used PCR amplification and agarose electrophoresis following the protocol by Fridolfsson and Ellegren (1999) to determine sex of the Lesser Black-backed Gull and the Herring Gull mate from 2011.

Data Analysis

Microsatellite DNA allele frequencies were calculated with Microsatellite Analyzer (MSA) software (Dieringer and Schlotterer 2003). We compared the multilocus genotype of the male LBBG by eye to the multilocus genotypes of all sampled chicks to determine if he could have been the male parent in years 2008–2010. We also included F07 in this analysis in 2011, the year we sampled the Herring Gull mate as well.

RESULTS

DNA Analyses

Allele frequencies (MSA) for 65 Appledore Herring Gulls are shown in Table 3. The multilocus genotypes of the Lesser Black-backed Gull, chick or egg tissues, and adult Herring Gull from 2011 are shown in Table 4. The LBBG has two alleles not found in the Appledore Herring Gull population: allele 138 at microsatellite locus La5ned and allele 269 at microsatellite locus Lm13pet (Table 4). One fledged chick (F04 from 2009) and one dead chick (from 2010) exhibited both of these ''private'' alleles of Lesser Black-backed Gulls in their multilocus genotypes.

Molecular sexing confirmed that the Lesser Black-backed Gull is a male and the Herring Gull mate in 2011 was a female.

Copulation Behavior

On numerous occasions, we observed the Lesser Black-backed Gull copulating with his mates each year.

Intermediate Phenotype of Offspring

One of the offspring (field readable band: F02; Table 1) was observed by members of the public

TABLE 4. The multilocus genotypes of the Lesser Black-backed Gull male (band code, F05), chick (F02, F03, F04, F06, F07) or egg tissues, and adult Herring Gull (K75). Alleles in the chicks presumed to originate from the Lesser Black-backed Gull are in bold.

Sample ID	Year sampled	La5ned	Lm25fam	Lm17vic	Lm23ned	Lm7fam	Lm13pet
F02	2008	134/136	165/170		192/194	254/262	265/267
F03	2008	134/136	165/170	182/182	192/194	254/262	265/267
F04	2009	136/**138**	159/165	182/182	192/194	254/262	267/**269**
F06	2009	134/136	161/170	182/182		254/262	265/267
Dead chick	2010	136/**138**	159/159	182/182	192/206	254/262	267/**269**
F07	2011	134/136	159/161	182/182	192/206	262/262	265/267
F05	2011	134/**138**	159/170	182/182	192/194	262/262	265/**269**
K75	2011	136/136	159/161	182/182	204/206	254/262	267/267

FIG. 1. Presumed Lesser Black-backed × Herring Gull hybrid (field readable band, F02) observed at (A) Provincetown, MA standing next to a Herring Gull (photo by B. Nikula) and (B) a landfill in Florida (photo by M. P. Harris).

after dispersing from Appledore Island. Both observers indicated that the bird initially attracted their attention because it looked like a hybrid gull (based on mantle color, leg color and body structure) (Fig. 1). On 13 December 2009 the bird was observed in Provincetown, MA (B. Nikula, pers. comm.). The observer indicated that the mantle was too pale for a Lesser Black-backed Gull, but the wings were shorter and the body was stockier than is typical for a Lesser Black-backed Gull (Fig. 1A). This gull was also observed at a landfill in Florida in February 2010 (M. P. Harris, pers. comm.; Fig. 1B). The observer indicated that F02 had an unusual appearance and stood out among the crowd of over 40,000 gulls (including ~200 Lesser Black-backed Gulls and ~600 Herring Gulls) at the landfill.

Another gull, banded as a chick (field readable band: J06) in 2009 near the nest of the Lesser Black-backed Gull, was seen by two separate observers on the coast of Alabama in 2010 (C. McCready, M. J. Iliff, pers. comm.) (Fig. 2). One observer suggested that the bird was a Lesser Black-backed Gull × Herring Gull hybrid based

FIG. 2. Presumed Lesser Black-backed × Herring Gull hybrid (field readable band, J06) standing next to a Laughing Gull (*Leucophaeus atricilla*) observed in coastal Alabama (photo by C. McCready).

on its coloration and body structure (M. J. Iliff, pers. comm.). Specifically, the base of the bill was black, rather than pale as is the case for Herring Gulls. Additionally, the bird was dark above and pale below (and pale-headed), a pattern typical of Lesser Black-backed Gulls rather than Herring Gulls. J06 was not identified as one of the two offspring of the Lesser Black-backed × Herring Gull pair in 2009. Instead, two chicks (field readable band: F04 and F06) were observed being fed by the Lesser Black-backed Gull at the nest after banding, confirming their status as offspring. J06 was banded near the nest but was not seen at the nest in subsequent observations.

DISCUSSION

In this study, we provided three lines of evidence that strongly suggest that a male Lesser Black-backed Gull produced viable hybrid offspring with at least two Herring Gulls on Appledore Island. First, analysis of microsatellite DNA is consistent with the Lesser Black-backed Gull siring all the chicks genotyped from the Lesser Black-backed Gull × Herring Gull nest between 2008–2011. Even more definitively, two offspring sampled (chick F04 from 2009 and embryonic tissue from 2010) each carried alleles (138 at locus La5 and 269 at locus Lm13) that to this point are specific to the Lesser Black-backed Gull male and have not been found in the Appledore Herring Gull population. We also observed the Lesser Black-backed Gull copulating with its mates each year. Third, one of the known offspring was observed after it dispersed from Appledore Island; it exhibited an intermediate phenotype, suggesting hybrid status. This study represents the first observed case of hybridization between these two species in North America. The formation of mixed pairs and the breakdown of isolating mechanisms are likely to occur when one species (in this case, Lesser Black-backed Gull) attaches itself to a colony where there are no conspecific mates available (Tinbergen 1953). Additionally, low levels of post-mating isolation may be a general phenomenon among large gulls (Gay et al. 2007).

The Herring Gull assemblage consists of more than 20 taxa, which occupy a circumpolar breeding range in the northern hemisphere. This assemblage has represented a significant systematic challenge because of the frequency of hybridization occurring between well-established species, the strong plumage similarity among some taxa, and the high level of phenotypic differentiation in some cases without apparent reproductive isolation (Crochet et al. 2002). Low levels of genetic differentiation at nuclear loci are thought to be explained by a combination of recent species origin and interspecific gene flow (hybridization) after speciation (e.g., Crochet et al. 2003, Sonsthagen et al. 2012).

The physical appearance of the Lesser Black-backed Gull in our study is consistent with the subspecies *L. f. graellsii*, and current thinking is that all, or almost all, North American Lesser Black-backed Gulls are this subspecies. However, it is not possible to conclusively eliminate *L. f. intermedius* as the subspecies because of the large amount of phenotypic variability among individuals of both subspecies. *L. fuscus graellsii* breeds in the Faroes, British Isles, Iceland, France, the Netherlands, Germany, and more recently the Canary Islands in the Macaronesian archipelago (Post and Lewis 1995, Grande and Palacios 2002). Numbers of this subspecies have increased substantially during the past decade (Hallgrimsson et al. 2011) and the breeding distribution has expanded to southwest Greenland (Boertmann 2008). It is quite possible that there are breeding populations of this subspecies in North America that have yet to be discovered.

A gull banded as a chick (band J06) in 2009 near the nest of the Lesser Black-backed Gull was resighted in coastal Alabama, USA, several months after it dispersed from Appledore Island. Based on its intermediate phenotype, this bird appeared to be a Herring Gull × Lesser Black-backed Gull hybrid. The bird was banded near the nest of the Lesser Black-backed Gull, but subsequent observations of the nest showed that it did not originate from the Lesser Black-backed Gull × Herring Gull pair. It is possible that this bird resulted from extra-pair copulation between the Lesser Black-backed Gull and a neighboring Herring Gull. Its phenotype was very similar to that of the confirmed offspring of the Lesser Black-backed Gull × Herring Gull, F02, also observed off the island. Compared to passerines, extra-pair paternity is low in seabirds, most likely because seabirds have long-term pair bonds with low divorce rates, very high paternal investment, and relatively small testes (Ashmole 1971, Furness and Monaghan 1987, Gilbert et al. 1998, Moller and Cuervo 2000).

There are several records of Herring Gulls breeding with other species of large white-headed gulls in North America including California Gulls, Glaucous-winged Gulls, Iceland Gulls, Glaucous Gulls, Thayer's Gulls, and Great Black-backed Gulls (McCarthy 2006). In a situation similar to the one we describe, Kelp Gulls, which are residents of South America, colonized islands off the coast of Louisiana in the early 1990s around the same time that the islands were colonized by Herring Gulls (Dittman and Cardiff 2005). Hybridization occurred, and now both parental types and hybrids breed at these islands.

Increasing numbers of observations of Lesser Black-backed Gulls, including observations of putative Lesser Black-backed Gull × Herring Gull hybrids, indicate that Lesser Black-backed Gulls may be in the process of colonizing North America. If this is the case, hybridization with Herring Gulls is likely in areas of overlap. Additional research is required to ascertain the frequency of hybrid pairings in North America and to determine whether the hybrid offspring documented in this study are fertile.

ACKNOWLEDGMENTS

We thank the staff of the Shoals Marine Laboratory for logistical assistance. Support for M. C. Stoddard was provided by the National Science Foundation's Research Experience for Undergraduates Program at the Shoals Marine Laboratory. Constructive feedback on the manuscript was provided by R. Bowie and an anonymous reviewer. This paper is contribution number 168, Shoals Marine Laboratory.

LITERATURE CITED

Ashmole, N. P. 1971. Sea bird ecology and the marine environment. Pages 223–286 *in* Avian biology (D. S. Farmer, D. S. King, and K. C. Parkes, Editors). Academic Press, New York, USA.

Boertmann, D. 2008. The Lesser Black-backed Gull, *Larus fuscus*, in Greenland. Arctic 61:129–133.

Calladine, J. 2004. Lesser Black-backed Gull *Larus fuscus*. Pages 242–261 *in* Seabird populations of Britain and Ireland (P. I. Mitchell, S. F. Newton, N. Ratcliffe, and T. E. Dunn, Editors). Poyser, London, UK.

Cramp, S. and K. E. L. Simmons. 1983. The birds of the western Palearctic, Volume III. Oxford University Press, Oxford, UK.

Crochet, P. A., J. D. Lebreton, and F. Bonhomme. 2002. Systematics of large white-headed gulls: patterns of mitochondrial DNA variation in western European taxa. Auk 119:603–620.

Crochet, P. A., J. J. Z. Chen, J. M. Pons, J. D. Lebreton, P. D. N. Hebert, and F. Bonhomme. 2003. Genetic differentiation at nuclear and mitochondrial loci among large white-headed gulls: sex-biased interspecific gene flow? Evolution 57:2865–2878.

Dieringer, D. and C. Schlotterer. 2003. Microsatellite analyser (MSA): a platform independent analysis tool for large microsatellite data sets. Molecular Ecology Notes 3:167–169.

Dittman, D. L. and S. W. Cardiff. 2005. Origins and identification of Kelp × Herring Gull hybrids. Birding: 266–276.

Edwards, J. L. 1935. The Lesser Black-backed Gull in New Jersey. Auk 52:85.

ELLIS, J. C., M. C. STODDARD, AND L. W. CLARK. 2008. Breeding by a Lesser Black-backed Gull (*Larus fuscus*) on the Atlantic coast of North America. North American Birds 61:546–548.

FOGARTY, B. 2009. A large late summer aggregation of Lesser Black-backed Gulls on Long Island, NY. Kingbird 59:337.

FURNESS, R. W. AND P. MONAGHAN. 1987. Seabird ecology. Chapman and Hall, New York, USA.

GAY, L., G. NEUBAUER, M. ZAGALSKA-NEUBAUER, C. DEBAIN, J. M. PONS, P. DAVID, AND P. A. CROCHET. 2007. Molecular and morphological patterns of introgression between two large white-headed gull species in a zone of recent secondary contact. Molecular Ecology 16:3215–3227.

GILBERT, L., T. BURKE, AND A. KRUPA. 1998. No evidence for extra-pair paternity in the Western Gull. Molecular Ecology 7:1549–1552.

GRANDE, J. M. AND C. J. PALACIOS. 2002. First breeding record of the Lesser Black-backed Gull in the Macaronesic archipelago, North Atlantic; a large spread in its breeding range. Waterbirds 25:388–389.

HALLGRIMSSON, G. T., N. D. VAN SWELM, H. V. GUNNARSSON, T. B. JOHNSON, AND C. L. RUTT. 2011. First two records of European-banded Lesser Black-backed Gulls *Larus fuscus* in America. Marine Ornithology 39:137–139.

HAMILTON, M. B., E. L. PINCUS, A. DI FIORE, AND R. C. FLEISCHER. 1999. Universal linker and ligation procedures for construction of genomic DNA libraries enriched for microsatellites. BioTechniques 27:500–507.

HARRIS, M. P., C. MORLEY, AND G. H. GREEN. 1978. Hybridization of Herring and Lesser Black-backed Gulls in Britain. Bird Study 25:161–166.

LIEBERS, D., P. DE KNIJFF, AND A. J. HELBIG. 2004. The Herring Gull complex is not a ring species. Proceedings of the Royal Society of London Series B-Biological Sciences 271:893–901.

MCCARTHY, E. M. 2006. Handbook of avian hybrids of the world. Oxford University Press, Inc., New York, New York, USA.

MOLLER, A. P. AND J. J. CUERVO. 2000. The evolution of paternity and paternal care in birds. Behavioral Ecology 11:472–485.

OLSEN, K. M. AND H. LARSSON. 2004. Gulls of Europe, Asia and North America. Christopher Helm, London, UK.

PIEROTTI, R. J. AND T. P. GOOD. 1994. Herring Gull (*Larus argentatus*). The birds of North America. Number 124.

POST, P. W. AND R. H. LEWIS. 1995. The Lesser Black-backed Gull in the Americas: occurrence and subspecific identity. Birding 27:282–290.

RUTT, C. 2009. Status and distribution of Lesser Black-backed Gull (*Larus fuscus*) in Pennsylvania. Pennsylvania Birds 23:143–147.

SEUTIN, G., B. N. WHITE, AND P. T. BOAG. 1991. Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology-Revue Canadienne De Zoologie 69:82–90.

SONSTHAGEN, S. A., R. T. CHESSER, D. A. BELL, AND C. J. DOVE. 2012. Hybridization among Arctic white-headed gulls (*Larus* spp.) obscures the genetic legacy of the Pleistocene. Ecology and Evolution 2:1278–1295.

STERNKOPF, V. 2011. Molecular Analysis in sea gulls (Laridae) to reveal genetically relationship and phylogeographic differentiation. Vogelwarte 49:175–177.

TINBERGEN, N. 1953. The Herring Gull's world: a study of the social behaviour of birds. Collins, London, UK.

VAN VLIET, G., B. MARSHALL, D. CRAIG, AND J. EGOLF. 1993. First record of nesting activity by a Lesser Black-backed Gull (*Larus fuscus*) in North America. Bulletin of the Pacific Seabirds Group 20:21.

WELCH, L., S. MELVIN, R. SCHAUFFLER, AND J. C. ELLIS. 2010. Maine 2008 coastwide censusfor gulls and cormorants. Maine Coastal Islands National Wildlife Refuge, U.S. Fish and Wildlife Service.

The Wilson Journal of Ornithology 126(2):345–352, 2014

Testing for Behavioral Lateralization in Observational Data: a Monte Carlo Approach Applied to Neck-looping in American Flamingos

Austin L. Hughes,[1,2] Jonathan Cauthen,[1] and Caroline Driscoll[1]

ABSRACT.—We applied a Monte Carlo approach to test for both individual and group level laterality preferences in neck looping by American Flamingos (*Phoenicopterus ruber ruber*) at rest. We found no evidence of individual or group-level preferences, contrary to the results of previous studies. In the present data, the appearance of bias tended to decrease as the number of observations increased, suggesting that apparent lateral bias may be largely because of stochastic error. Pair members tended to loop the neck

[1] Department of Biological Sciences, Coker Life Sciences Building, 715 Sumter Street, University of South Carolina, Columbia, SC 29208, USA.

[2] Corresponding author; e-mail: austin@biol.sc.edu

to the same side on the same day to a greater extent than expected by chance, implying that social factors can act contrary to any individual lateral preference that may exist in this species. *Received 7 August 2013. Accepted 31 December 2013.*

Key words: flamingo, laterality, social dominance.

There has been considerable interest in lateralization of animal behaviors, in part because of its connection with brain lateralization (Harris 1989, Rogers 1989, Bisazza et al. 1998, Vallortigara 2000, Rogers et al. 2013). Behavioral lateralization can be defined as preferential use of one of two paired sensory organs or appendages, or preferential use of one direction (left or right) in locomotion or in other behaviors with a directional component. Behavioral lateralization may exist at the level of the individual (i.e., an individual deviation from equal preference) or of the social group or population (i.e., a group-wide or population-wide deviation from equal preference). Both kinds of lateralization can be detected in experimental paradigms or by observation in a wild or captive setting (Rogers et al. 2013). In either case, preferences are typically detected statistically by the Sign Test or similar tests of the hypothesis that a binomial probability is equal to 50%, with a significant deviation from 50% being taken as evidence of laterality.

A possible example of behavioral laterality in birds involves the direction in which American Flamingos (*Phoenicopterus ruber ruber*) loop the neck when resting with the head on the back and the bill tucked under the base of the wing (Anderson et al. 2009). An observational study reported significant individual lateral bias in neck-looping direction in 5 of 17 individuals in a captive population, as well as significant group-level rightward preference (Anderson et al. 2009). Using the same captive population, Anderson and colleagues (2010) also reported that individuals showing a preference for resting the neck toward the left were more likely to be involved in "aggressive" (i.e., agonistic) encounters. Anderson et al. (2010) suggested that a common underlying neural asymmetry may be responsible for both left-directing neck-looping and increased aggression, consistent with studies showing lateralization of agonistic behavior in several vertebrate species (Deckel 1995, Robins et al. 1998, Austin and Rogers 2007). Anderson et al. (2010) counted the number of times each individual was involved in an agonistic encounter without determining dominance, but there is evidence that captive groups of flamingos form stable dominance hierarchies (Hughes et al. 2013). The role of each participant in an agonistic encounter is expected to differ depending on the relative social dominance of individuals (Rowell 1974).

Like that of Anderson et al. (2009), studies of behavioral laterality of animals in groups frequently test simultaneously for both individual and group level preferences. In the analysis of such data, each individual's observed behavior is best treated as a sample from the same underlying null distribution, an aspect of testing for laterality in groups which is poorly captured by conducting independent statistical tests on each individual. In addition, each individual's behavior may not be strictly independent of the behavior of other group members because of social influences. Here, we apply a more rigorous approach to testing for both individual and group biases in neck-looping behavior of captive American Flamingos, using more extensive observations on a substantially larger number of individuals than provided by Anderson et al. (2009).

We used a Monte Carlo approach to test for both individual and group-level laterality, and compared the results to those of independent statistical tests on individual animals. Because we had over a year's worth of observations of dominance relations prior to the study of lateral bias, we were able to test for associations between laterality and dominance. Because we knew the identity of breeding pair members, we also tested for resemblance in neck-looping positions between members of the same pair, on the hypothesis that a mate's behavior might be one social factor influencing an individual's neck-looping position.

METHODS

Study Population.—Anderson et al. (2009) observed neck loop position of 40 resting adult American Flamingos at Riverbanks Zoo and Garden in Columbia, South Carolina, USA. Birds were marked with numbered leg bands. Data for 25 males and 15 females were included in the analyses reported here. The age range of these birds at the start of the study 2–45 years; mean = 14.6 ± 1.8 SE. The group observed included one other adult male which was never observed resting with his neck looped and was therefore

excluded from analyses. There was also one juvenile hatched in spring 2012 which was excluded from analyses because of our lack of observations of its dominance interactions. For more details on this population, see Hughes et al. (2013).

Measures of Laterality.—Observations of neck-resting position were made on 69 separate days 23 October 2012–18 July 2013. Daily observation periods ranged in length from 45–180 min, and the total observation time amounted to 93 hrs. Although Anderson et al. (2013) did not mention the length of their observation periods, their observations were confined to 40 days over 3 months. Here, we use the definition that $L_{ij} = 1$ and $R_{ij} = 0$ if the ith bird was seen resting with its neck looped to the left only on the jth day. Likewise, we define $R_{ij} = 1$ and $L_{ij} = 0$ if the ith bird was seen resting with its neck looped to the right only on the jth day. If at different times on the jth day, the ith bird was seen resting with its neck looped to both the left and to the right, then let $L_{ij} = 0.5$ and $R_{ij} = 0.5$. Let $L_{i.}$ = the sum for all j of the L_{ij}, and let $R_{i..}$ = the sum for all j of the R_{ij} Thus, $L_{i.} + R_{i..}$ will equal N_i, the number of days on which the ith bird was observed resting with its neck looped. Let $pR = R_{i.}/N_i$; that is, the proportion of days in which the bird rested with its neck looped to the right; and $pL = 1 - pR$. Likewise, let $bR = (R_{i..} - L_i)/N_i$; bR is the measure of individual rightward lateral bias used by Anderson et al. (2009). Let $L_{..}$ = the sum of $L_{i.}$ across all birds, and let $R_{..}$ be the sum of $R_{i..}$ across all birds. For all birds, let $pR = R_{..}/(R_{..} + L_{..})$, and $pL = 1 - pR$. The Shannon (1948) index of entropy (H) is defined by

$$H = pR\{\log_2(pR)\} + pL\{\log_2(pL)\}$$

H is a measure of randomness, which takes a maximum value (in this case 1.0), when $pR = pL = 0.5$. Let $L_{..}$ = the sum of $L_{i.}$ across all birds, and let $R_{..}$ be the sum of $R_{i..}$ across all birds.

Agonistic and Pairing Behaviors.—Dominance relations of the 40 birds were assessed on the basis of observations conducted 10 September 2011–31 August 2012 on the same group. We used dominance scores based on these earlier observations in order to avoid possible bias that might be introduced by using observations contemporaneous with those of neck-resting position, since resting individuals would by definition not be involved in agonistic encounters. However, we recorded dominance encounters during the period when neck-looping observations were made, and dominance relations were highly stable between the two periods. Observations were made on a total of 134 hrs of observation on 101 separate days. Dyadic agonistic encounters included the following: (1) less escalated encounters involving neck-swaying threats (Kahl 1975), usually accompanied by vocalizations; and (2) more escalated encounters involving pecking, biting, and attempts by the birds to get hold of each other's mandibles (Schmitz and Baldassarre 1992). We were able to determine the band number of both birds in the case of 3,595 encounters.

Agonistic encounters were scored as *resolved* if one bird showed clear dominance to the other, with the subordinate withdrawing or fleeing from the encounter; other agonistic encounters were considered *unresolved*. If more than two birds were involved in an agonistic encounter, each bird was counted as being involved in a separate agonistic encounter for each bird with which it interacted directly. Bouts of agonistic behavior separated by 1 min or more were counted as separate encounters. As a cardinal measure of each individual's dominance, we used the dominance index (*DI*) computed as the proportion of resolved encounters that an individual won. For the 40 birds used in analyses, *DI* was strongly positively correlated ($r = 0.988$; $P < 0.001$) with the normalized David's score (*DS*; De Vries et al. 2006). *DS* makes use of information on the dominance of individuals with which an individual interacts, but because group membership had changed after deaths since the period when observations on agonistic encounters were made, *DI* seemed a more appropriate measure to use for tests of relationships with lateral bias.

The birds included in our observations included 14 pairs, 12 male-female pairs and 2 male-male pairs, which were observed repeatedly together, often resting side by side, and during the nesting season were involved together in nest-mound building or in competition over nest mounds. Nesting took place May–June 2013. In order to maximize egg survival, zoo personnel replaced eggs with dummy eggs, while the eggs were incubated artificially. When young ($n = 3$) hatched, the eggs were placed in nests attended by pair members judged to be assiduous in incubation and therefore likely to be successful parents. The pairs whose dummy eggs were replaced by live young were not necessarily the parents of the young, which were unknown.

Statistical Methods.—For each individual bird, the null hypothesis that $L_{i.} = R_{i.}$ (i.e., $pR = pL = 0.5$) was tested by two-tailed Sign Tests (assuming a binomial distribution; Hollander and Wolfe 1973). Sign Tests were conducted two ways: (1) without correction for multiple testing, as in Anderson et al. (2009); and (2) using the Bonferroni correction for multiple testing. In addition, hypotheses regarding the mean and range of *pR* were tested by a Monte Carlo procedure, which involved creating 1,000 simulated populations, each containing the same number of individuals as the real population and having a distribution of N_i values identical to the real population. By mimicking the distribution of N_i values in the real population, these simulations enabled us to ask whether the mean value and individual values, particularly the extreme values (minimum and maximum), in the real population were more extreme than expected to occur under the null hypothesis. For a two-tailed test, a value was considered significant at the 5% level if it was less than the 2.5-percentile of the distribution generated by the 1,000 simulated populations or greater than the 97.5-percentile of the distribution generated by the simulated populations. The *pR* values for each individual in the simulated populations were created by sampling from a binomial distribution with probability of "success" equal to the value of *pR* under the null hypothesis being tested. These same analyses were applied both to our study population and to the data of Anderson et al. (2009).

We tested for associations between *DI*, numbers of agonistic encounters, and variables associated with laterality of neck looping using Pearson's correlation test. Statistical analyses were conducted in Minitab version 15 (www.minitab.com; Meyer and Krueger 2001). All reported *P*-values are two-tailed.

RESULTS

Patterns of Neck-Looping.—Out of 69 days of observations, the mean number of days on which the 40 American Flamingos were observed resting with their necks looped (N_i) was 34.8 ± 1.4 SE (median = 35; range 15–54 days). The mean *pR* was 0.486 ± 0.015 SE, with a median of 0.478 and individual *pR* values ranging from 0.291–0.711. The mean *bR* was −0.029 ± 0.030 (range −0.419–0.421). Thus, our study group showed a slight overall leftward bias, in contrast to the rightward bias seen in the group studied by Anderson et al. (2009), where the mean *pR* was 0.583 ± 0.028, and mean *bR* was 0.165 ± 0.056.

All 40 birds in our population were seen resting with the neck looped toward the right and toward the left on the same day at least once. The mean number of days on which an individual bird was observed assuming both resting positions was 7.4 ± 0.8 (range 1–30 days). The mean percentage of N_i on which both resting positions were observed was 19.7 ± 1.6% (range = 4%–55.6%). There was a significant positive correlation between the number of days on which a bird was observed resting with its neck looped and the percentage of days on which it was observed assuming both positions ($r = 0.586$; $P < 0.001$).

A time-series plot of *pB* for all birds in the group showed wide and apparently random day-to-day fluctuations (Fig. 1A). On the other hand, a time-series plot of cumulative *pB* over the course of the study showed an initial pattern of wide fluctuation with a gradual leveling off at a value close to the overall mean *pB* (Fig. 1B). Likewise, cumulative *H* leveled off at a high value, close to the maximum possible value of 1.0, after an initial decline and wide fluctuation (Fig. 1C). Thus, the cumulative data on neck-looping position showed increased randomness over the course of the study after an initial apparent decrease in randomness.

Tests of Lateral Bias.—In individual Sign Tests, four of the 40 birds showed significant ($P < 0.05$) deviations from the null expectation that $pR = 0.5$; three of these were left-biased and one right biased. However, when the conservative Bonferroni correction for multiple testing was applied, none of the birds showed a significant bias. In the data of Andersson et al. (2009), 4 of 17 birds showed significant ($P < 0.05$) deviations from $pR = 0.5$ in individual Sign Tests. Applying the Bonferroni correction, two of these birds continued to show significant deviations from the null expectation.

The results for our population were compared with 1,000 Monte Carlo simulated populations of 40 flamingos with the distribution of days observed the same as in our population and expected $pR = 0.5$. The mean, minimum, maximum, and range of *pR* in our population showed no significant differences from the random expectation based on these simulations. For example, the range in individual *pR* values in the observed data (0.420) fell at about the 70

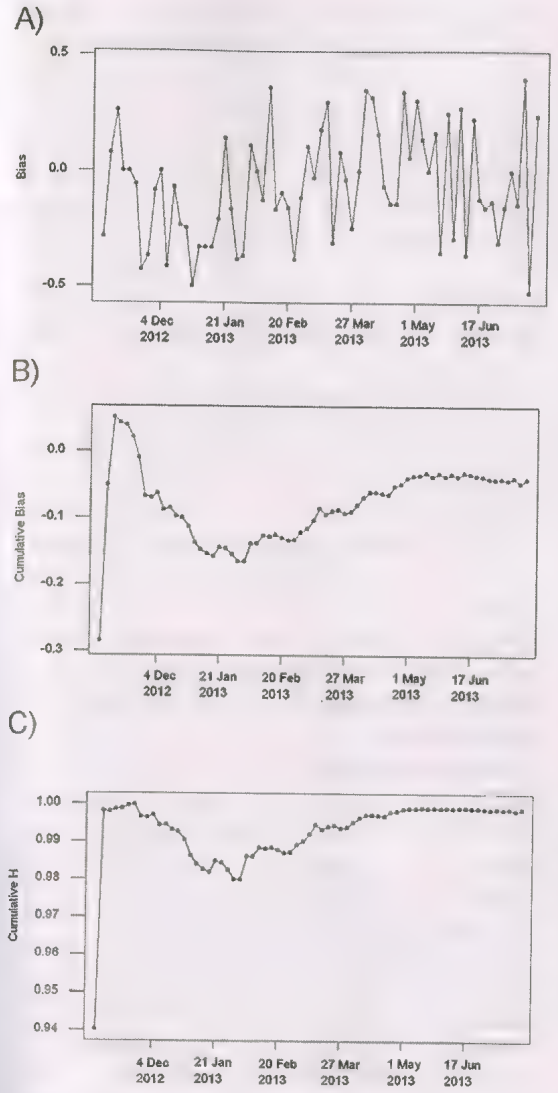


FIG. 1. Time series plots of (A) bias (*bR*); (B) cumulative bias; and (C) cumulative entropy (*H*) of neck-looping position in a group of 40 American Flamingos.

percentile of the ranges found in the 1,000 simulated populations (Fig. 2). Deviation of the minimum, maximum, and range in the observed data from those in the simulations provided a test of the hypothesis that certain individuals have lateral preferences deviating from the null expectation, since extreme values would affect those statistics. Thus, the simulation results implied that neither the population as a whole nor any individual bird showed any significant deviation from what was expected if there is no lateral preference in neck-resting posture.

We likewise simulated 1,000 populations of 17 flamingos with the distribution of days observed the same as in Anderson et al. (2009) and expected $pR = 0.5$. In this case, the observed pR was highly significantly different from the expectation based on the simulations ($P < 0.002$). However, the minimum and range did not differ significantly from the expectation based on the simulation.

We then simulated 1,000 populations of 17 flamingos with the distribution of days observed the same as in Anderson et al. (2009) and expected $pR = 0.583$, the mean pR observed by those authors. In the latter case, mean, minimum, maximum, and range of pR observed in Anderson et al.'s (2009) population showed no significant differences from the random expectation based on these simulations. Thus, in the case of Anderson et al.'s (2009) data, the simulation results implied that, while there was a significant rightward bias of the population as a whole, no individual bird showed significant deviation from what was expected given the population bias.

Relationship with Agonistic Behavior.—The dominance index (*DI*) was not significantly correlated with *bR* ($r = -0.005$; n.s.) or with *H* ($r = 0.032$; n.s.). However, *DI* was significantly positively correlated with N_i; i.e., the number of days on which a bird was observed resting with its neck looped ($r = 0.409$; $P = 0.009$). The total number of agonistic encounters observed (both resolved and unresolved) was not significantly correlated with *bR* ($r = -0.015$; n.s.), with H ($r = 0.001$; n.s.), or with N_i ($r = 0.245$; n.s.).

Pair Members.—We compared the number of days on which both members of a pair were observed resting with their the necks looped in the same direction with the random expectation based on each bird's observed *pL* and *pR* (Fig. 3). For both left-side and right-side neck-looping, the observed values were always greater than the expected values, sometimes substantially so (Fig. 3). The mean number of days on which both pair members were observed resting with the neck looped on the left side was 10.6 ± 1.4, while the mean of the expectations was 7.5 ± 1.3. These means were significantly different (paired *t*-test; $P < 0.001$). The mean number of days on which both pair members were observed resting with the neck looped on the right side was 10.1 ± 1.0, while the mean of the expectations was 6.4 ± 0.8. Again the means were significantly different (paired *t*-test; $P < 0.001$).

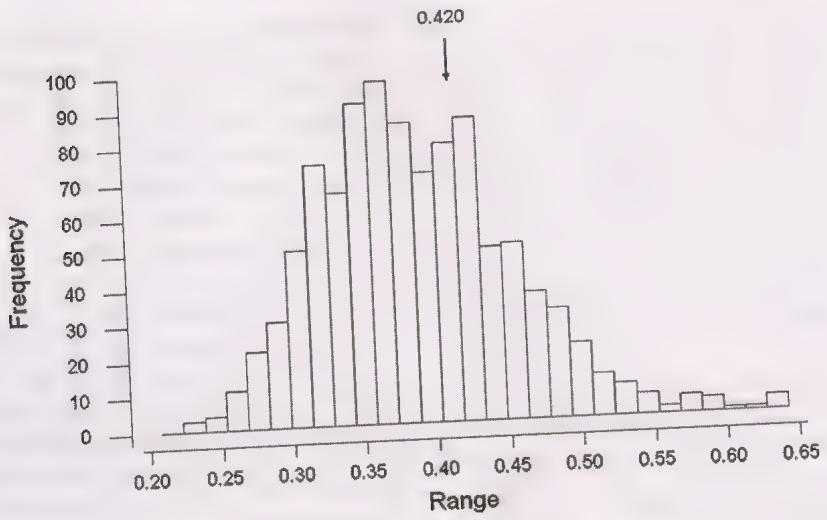


FIG. 2. Distribution of the range (highest minus lowest) of *pR* values in 1,000 simulated populations; *arrow* indicates the value in the real population.

DISCUSSION

Observations on neck-looping behavior in a captive group of American Flamingos provided no support for the hypothesis that either the group as a whole or any individual bird had significant lateral bias in the choice of neck-resting posture, contrary to the finding of Anderson et al. (2009) on another captive group of the same species. Computer simulations taking into account differences among individuals with respect to the number of observations showed no evidence that the observed pattern of neck-resting postures in different group members was any different from expected under the absence of any lateral preference. There was an appearance of nonrandomness early in the study, but this appearance eventually disappeared as more observations were gathered (Fig. 1).

When applied to the data of Anderson et al. (2009), our computer simulation approach provided no evidence of individual lateral bias, although it did suggest an overall rightward bias in the group studied by those authors. By contrast, individual Sign Tests supported significant bias in two birds from Anderson et al.'s (2009) data set, even when corrected for multiple testing by the conservative Bonferroni procedure. It is difficult to speculate on the causes of the group bias

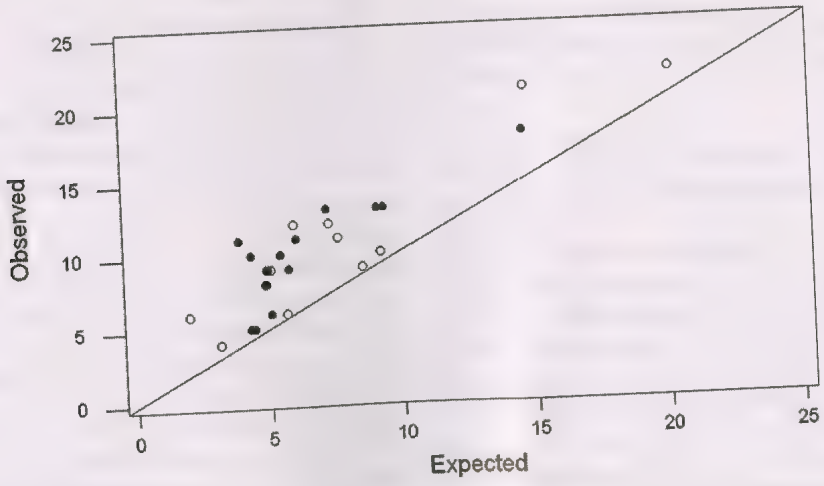


FIG. 3. Observed number of days on which pair members were both observed with the neck looped to the right (*solid circles*) and to the left (*open circles*) plotted as a function of expected numbers of days. The line is a 45° line.

observed in Anderson et al.'s (2009) study and confirmed here even by the conservative Monte Carlo approach. One difference between the two groups was the substantially more male-biased sex ratio in our population (1.67 males:females) in comparison to Anderson et al.'s (2009) population (0.7). Differences in exhibit design, possibly giving rise to differences in micro-climate, might also have contributed.

Nonetheless, it is possible that the apparent individual and group biases observed by Anderson et al. (2009) may have resulted from stochastic error. The maximum number of days for which data on neck-looping were obtained for an individual bird in Anderson et al.'s (2009) study was 36 days. In our study we obtained 36 or more days of neck-looping observations on a total of 19 individuals, with a maximum value of 54 days. The absence of observed bias in the larger data set suggests a role for stochastic error in the smaller data set. Consistent with this interpretation was the decrease in apparent bias over time in the present data, as well as the significant positive correlation between the number of days on which a bird was observed resting with its neck looped and the percentage of days on which it was observed resting with the neck looped in both positions.

We found no correlation between neck-looping bias and social dominance index or the number of agonistic encounters. However, dominance index was positively correlated with the number of days on which a bird was observed resting with its neck looped. The latter observation may be explained on the hypothesis that dominant individuals are more secure and thus likely to spend more time resting than do subordinate individuals that may frequent the enclosure out of fear of attack. Indeed, it was not uncommon in our study group to observe a resting subordinate individual assume a vigilant posture and/or withdraw from the area when a dominant individual approached.

Our data showed a generally slight but consistent trend for pair members to share neck-looping position on a given day to a greater extent than expected by chance. Since pair members frequently rested side-by-side, a tendency to loop the neck in the same direction may often be favored by considerations of available space alone. Alternatively, similar neck-looping may be an aspect of pair-bond maintenance, as with parallel postures in the Galah (*Eolophus roseicapilla*, Psittaciformes; Rogers and McCulloch 1981). In either case, our results imply that pair members can influence each other's patterns of neck-looping, in turn suggesting that social factors can act contrary to any individual lateral preference that may exist in this species.

When behavioral observations are used to test for lateral bias, each individual's totals can be viewed under the null hypothesis as a sample drawn from a common binomial distribution. Because each individual represents a finite sample from that underlying distribution, deviation from left:right equality will occur in certain individuals by chance alone. The Monte Carlo approach used here takes such stochastic variation into account, thereby providing a more robust test of lateral bias than separate tests applied to individual birds. By taking into account differences among birds with respect to the numbers of observations, this method provides a more conservative test of the hypothesis of individual bias than the Bonferroni correction applied to separate tests. The Monte Carlo approach used here can be applied to any observational study of lateral bias in either captive or wild groups of animals, providing a simple means of formulating and testing a null hypothesis regarding both individual-level and group-level lateral bias.

ACKNOWLEDGMENTS

We are grateful to the Riverbanks Zoo bird department and hospital staff for their work in managing the birds, especially senior bird keeper Kate-Lyngle Cowand, bird keeper Christine Talleda, senior veterinarian Keith Benson DVM, and associate veterinarian Cora Singleton DVM.

LITERATURE CITED

Anderson, M. J., S. A. Williams, and E. H. O'Brien. 2009. Individual differences in the preferred neck-resting position of Caribbean Flamingos (*Phoenicopterus ruber*). Laterality 14:66–78.

Anderson, M. J., S. A. Williams, and A. J. Bono. 2010. Preferred neck-resting position predicts aggression in Caribbean Flamingos (*Phoenicopterus ruber*). Laterality 15:629–638.

Austin, N. P. and L. J. Rogers. 2007. Asymmetry of flight and escape turning responses in horses. Laterality 15:464–474.

Bisazza, A., L. J. Rogers, and G. Vallortigara. 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles, and amphibians. Neuroscience and Behavioral Reviews 22:411–426.

Deckel, A. W. 1995. Lateralization of aggressive responses in *Anolis*. Journal of Experimental Zoology 272:194–200.

De Vries, H., J. M. Stevens, and H. Vervaeke. 2006. Measuring and testing the steepness of dominance hierarchies. Animal Behaviour 71:585–592.

Harris, L. J. 1989. Footedness in parrots: three centuries of research, theory, and mere surmise. Canadian Journal of Psychology 43:369–396.

Hollander, M. and D. A. Wolfe. 1973. Nonparametric statistical methods. Wiley, New York, USA.

Hughes, A. L., A. Raynes, C. Driscoll, and J. Babler. 2013. Behavioral correlates of post-breeding weight change in a captive flock of American Flamingos (*Phoenicopterus ruber ruber*). Zoo Biology 32:204–209.

Kahl, M. P. 1975. Ritualized displays. Pages 142–149 *in* Flamingos (J. Kear and N. Duplaix-Hall, Editors.), Poyser, Berkhamsted, UK.

Meyer, R. and D. Krueger. 2001. Minitab guide to statistics. Second Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Robins, A., G. Lippolis, A. Bisazza, and G. Vallortigara. 1998. Lateralized agonistic responses and hindlimb use in toads. Animal Behaviour 56:875–881.

Rogers, L. J. 1989. Laterality in animals. International Journal of Comparative Psychology 3:5–25.

Rogers, L. J. and H. McCulloch. 1981. Pair-bonding in the Galah, *Cacatua roseicapilla*. Bird Behavior 3:80–92.

Rogers, L. J., G. Vallortigara, and R. J. Andrew. 2013. Divided brains: the biology and behaviour of brain asymmetries. Cambridge University Press, Cambridge, UK.

Rowell, T. 1974. The concept of social dominance. Behavioral Biology 11:131–154.

Schmitz, R. A. and G. A. Baldassarre. 1992. Contest asymmetry and multiple bird conflicts during foraging among nonbreeding American Flamingos in Yucatan, Mexico. Condor 94:254–259.

Shannon, C. 1948. A mathematical theory of communication. Bell System Technical Journal 27:79–423, 623–656.

Vallortigara, G. 2000. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. Brain and Language 73:189–210.

The Wilson Journal of Ornithology 126(2):352–359, 2014

Dispersal Patterns Suggest Two Breeding Populations of Piping Plovers in Eastern Canada

Diane L. Amirault-Langlais,[1,3,5] Tara L. Imlay,[2,4] and Andrew W. Boyne[2]

ABSTRACT.—Piping Plovers (*Charadrius m. melodus*) were banded in eastern Canada, in the Gulf of St. Lawrence (Gulf) region, including the Magdalen Islands (Québec), New Brunswick, Newfoundland, northern Nova Scotia and Prince Edward Island, and the southern Nova Scotia (sNS) region from 1998–2003, and recaptured and/or resighted from 1999–2007. Return rates of banded individuals were greater for adults than juvenile birds, likely reflecting the higher survival and site fidelity of this age class. The best-fit model explaining differences in annual dispersal distance included age class ($P < 0.001$), region ($P = 0.004$) and the interaction of age class and region ($P = 0.074$). Juvenile dispersal movements in the Gulf (median: 28.0 km, range: 0.4–306.3 km) were greater than in sNS (median: 18.6 km, range: 6.5–74.8 km), but adult movements in sNS (median: 4.0 km, range: 0.01–70.7 km) were greater than in the Gulf (median: 0.5 km, range: 0.01–298.6 km). While some annual dispersal movements in the Gulf were large enough to cover the distance between both regions (>225 km), these movements only represented 1% of all observations and none involved movements between the Gulf and sNS. The lack of movement between regions, and previous studies documenting differences in population dynamics and habitat use, suggests that two distinct breeding populations of Piping Plovers exist in eastern Canada. Future management of the species should consider the distinct conservation needs of both populations and recognize that local efforts may not result in regional population increases because of small dispersal distances in eastern Canada, and, potentially, in other populations in North America. At this time, the small sNS population may be particularly vulnerable to

[1] Canadian Wildlife Service, Atlantic Region, Environmental Stewardship Branch, Environment Canada, 17 Waterfowl Lane, Sackville, NB E4L 1G6, Canada.

[2] Canadian Wildlife Service, Atlantic Region, Environmental Stewardship Branch, Environment Canada, 45 Alderney Drive, 16th floor, Dartmouth, NS B2Y 2N6, Canada.

[3] Current address: Kouchibouguac National Park, 186 Route 117, Kouchibouguac NB E4X 2P1, Canada.

[4] Current address: Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax NS B3H 4J1, Canada.

[5] Corresponding author;
email: diane.amirault-langlais@pc.gc.ca

extirpation, as the potential for dispersal from nearby populations appears limited. *Received 4 April 2013. Accepted 7 December 2013.*

Key words: Piping Plover, *Charadrius melodus*, eastern Canada, dispersal, population, species at risk, conservation.

Piping Plovers (*Charadrius m. melodus*) are listed as endangered in eastern Canada (Environment Canada 2012) and threatened along the Atlantic coast of the United States (USFWS 1986). Research to describe dispersal and site fidelity of Piping Plovers (*C. m. melodus* and *C. m. circumcinctus*) has been conducted across the North American breeding range (Wilcox 1959; Cairns 1982; Haig and Oring 1988a, b; Knetter et al. 2001; Cohen et al. 2006; Catlin 2009; LeDee et al. 2010; Cohen and Gratto-Trevor 2011; Rioux et al. 2011; Hillman et al. 2012; Roche et al. 2012) and overwintering range (Drake et al. 2001, Gratto-Trevor et al. 2012). Previous studies have demonstrated that dispersal is influenced by breeding success, with unsuccessful plovers being more likely to disperse (Roche et al. 2012) and travel significantly greater distances than successful conspecifics (Rioux et al. 2011). Rioux et al. (2011) also demonstrated that the poor breeding success of nearby pairs increased dispersal distances. The availability of suitable habitat (Catlin 2009) and flooding events (Roche et al. 2012) can also influence dispersal.

To date, there has been relatively little research targeted on the population in eastern Canada. Cairns (1982) published the results of a study conducted at Cadden Beach, Nova Scotia; however, this research focused on a small proportion of the breeding range and did not permit a comprehensive understanding of the extent of dispersal. Rioux et al. (2011) documented the influence of breeding success on dispersal in eastern Canada, but this work also did not address the extent of these movements. The need to understand the extent of adult and juvenile dispersal in eastern Canada is particularly important as this population has failed to show demonstrable recovery despite reporting consistently high productivity rates (Hecht and Melvin 2009) and considerable conservation efforts (Gratto-Trevor and Abbott 2011). This trend is puzzling as productivity rates reported for eastern Canada (average 1.61 chicks fledged/pair, Hecht and Melvin 2009) are among the highest of any North American population of Piping Plovers (summarized in Haig and Elliott-Smith 2004, Haig et al. 2005, Hecht and Melvin 2009, Goossen and Amirault-Langlais 2010). Large population increases have been documented along the U.S. Atlantic coast with lower productivity (average 1.19–1.44 chicks fledged/pair within U.S. Atlantic coast recovery units, Hecht and Melvin 2009), while over the same time period, the population size of Piping Plovers in eastern Canada has decreased (Elliott-Smith et al. 2009; Hecht and Melvin 2009; Goossen and Amirault-Langlais 2010; AWB, unpubl. data). Emigration of Piping Plovers from eastern Canada to other populations along the Atlantic coast has been suggested to explain the contrasting population trends. However, Miller et al. (2010) found evidence of genetic structure among individuals from the *melodus* subspecies, indicating low rates of long-distance dispersal.

In order to address questions raised by the lack of demonstrable recovery in eastern Canada, we implemented research aimed at gaining a better understanding of dispersal. In eastern Canada, breeding Piping Plovers are distributed along the Atlantic coast (in southern Nova Scotia) and the Gulf of St. Lawrence. The closest breeding beaches between these two areas are only separated by ~100 km over land but are much farther apart via the coast. Furthermore, the areas are exposed to different coastal regimes, resulting in differences in the habitat characteristics of beaches along these bodies of water. In general, beaches along the Gulf are wider, with a lower slope and a higher proportion of mixed (both cobble and sand) substrate than those along the Atlantic Coast (Boyne et al. in press). The goal of this study was to characterize and compare the extent of annual dispersal of juvenile and adult Piping Plovers in eastern Canada. We also assessed breeding population connectivity within eastern Canada and with the U.S. Atlantic coast population.

METHODS

Field Methods.—We conducted a band-resighting study from 1998–2003 in two regions of eastern Canada: the Gulf of St. Lawrence or 'Gulf' (containing beaches in New Brunswick [NB], Newfoundland [NL], northern Nova Scotia [nNS], Prince Edward Island [PE] and the Magdalen Islands, Québec [QC]) and southern Nova Scotia or 'sNS' (Fig. 1). We used a box trap or modified Weller trap (Weller 1957) to capture nesting adult Piping Plovers while they incubated, and we captured unfledged juvenile birds with a small net. With one exception, each plover

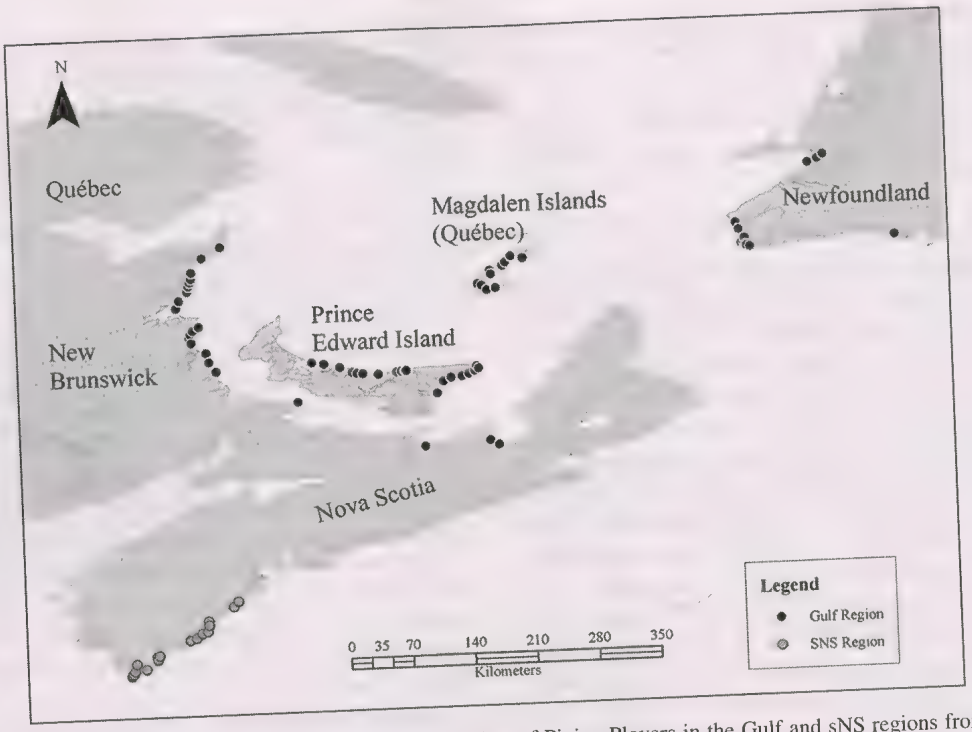


FIG. 1. Location of banding and resighting/recapture sites of Piping Plovers in the Gulf and sNS regions from 1998–2003.

received a single band on each tarsometatarsus – an incoloy or stainless steel United States Geological Survey (USGS) band (plovers banded in QC in 1998 received this band on the tibiotarsus), and a plastic (1998–2000) or anodized aluminum (2001–2003) color band specific to the province of capture on the opposite leg. The aluminum color bands also had unique alpha codes, enabling identification of individuals from a distance. The USGS band was placed on the right leg of adults, whereas juveniles received the USGS band on the left leg.

During the study, we banded 887 Piping Plovers (Table 1). The initial banding scheme

TABLE 1. Summary of Piping Plovers banded in eastern Canada (1998–2003) by province and region and the proportion of those recaptured or resighted in at least one year post-banding (1999–2007).

				# resighted in each province					
Province banded[a]	Age class	# banded	# resighted (%)	NB	NL	nNS	PE	QC	sNS
NB	Adult	89	26 (29.2)	26	-	-	-	-	-
	Juvenile	166	23 (13.9)	20	1	1[b]	2[b]	-	-
NL	Adult	34	11 (32.4)	-	11	-	-	-	-
	Juvenile	53	6 (11.3)	-	6	-	-	-	-
nNS	Adult	12	6 (50.0)	-	-	5	1	-	-
PE	Adult	69	41 (59.4)	1	-	3	37	-	-
	Juvenile	110	16[c] (14.5)	2	-	-	9	3	-
QC	Adult	62	43 (69.4)	-	1	-	3	39	-
	Juvenile	95	16 (16.8)	1	1	-	1	13	-
sNS	Adult	63	32 (50.8)	-	-	-	-	-	32
	Juvenile	134	31 (23.1)	-	-	-	-	-	31

[a] Abbreviations for provinces: NB = New Brunswick, NL = Newfoundland, nNS = northern Nova Scotia, PE = Prince Edward Island, QC = Quebec (Magdalen Islands), sNS = southern Nova Scotia.
[b] One juvenile banded in NB was resighted 2 years later breeding in PE and staging in nNS.
[c] One juvenile banded in PE was resighted the following years in New York and Massachusetts.

(1998–2000) lacked individual identification; therefore, recapture was necessary to identify individuals. Coded aluminum bands were used from 2001–2003, so individuals could be identified without being recaptured. Birds were recaptured and resighted throughout the study (1998–2003), and incidental sightings continued until 2007. All beaches with suitable habitat were surveyed at least once, ideally twice, between late April and mid-May to confirm the presence of nesting pairs on a beach. Frequent surveys of suitable habitat continued until 1 July to locate birds that may move to re-nest. Once the presence of pairs was confirmed, we conducted follow-up visits to accurately determine productivity and identify returning adults or to band adults and young. Remote sites (i.e., northern NB and NL) were often surveyed less frequently than those with easier access.

Efforts to identify banded individuals following 2003 were exclusively focused on recapturing individuals and removing anodized aluminum color bands, which had caused injuries to some individuals (Amirault et al. 2006b). The breeding behavior of birds with band injuries was consistent with the behavior of non-injured plovers (Amirault et al. 2006b); therefore, 17 injured individuals were included in the analysis on annual dispersal distances described below. A detailed description of the protocol used during the research program is presented in Amirault et al. (2006a).

Statistical Analysis.—We summarized the number of birds banded from 1998–2003, and recaptured or resighted from 1999–2007. A Chi-square test was used to determine if there was a difference in return rates (determined through the recapture and/or resighting of banded individuals) between birds banded as juveniles and adults in the Gulf and sNS regions. Expected return rates were calculated by multiplying the number of birds banded in each age class and region by the overall return rate. The overall return rate (28%) was determined by dividing the number of recaptured or resighted birds (251) by the total number banded (887).

Global positioning system (GPS) coordinates were recorded for most nest sites where adults and juveniles were banded, resighted and/or recaptured from 2001–2006. In some cases, banded birds were only resighted after the young had hatched; therefore, the nest coordinates were unknown. The resighting location was recorded for these individuals from the areas where the adult was first observed with the chicks. We assumed that nesting occurred on the same beach, given that chicks were captured on average 170 ± 139 (SD) m from their nest, and parents typically tend to their chicks closely. Precise coordinates were not available for most birds banded and resighted from 1998–2000. Individuals without precise nest and resighting coordinates were not included in the analysis of annual dispersal distances. Annual dispersal distance was defined as the distance between nest and resighting locations in two consecutive breeding seasons. We calculated median annual dispersal distances for birds banded as juveniles and adults that were resighted in consecutive years in both the Gulf and sNS regions.

Calvert et al. (2006) estimated the probability of second-year birds being recruited into the breeding population as 0.8095 and 0.8504 for the Gulf and sNS, respectively – suggesting that some juveniles may not breed until their third year. Survey coverage in most areas of eastern Canada is extensive, particularly in sNS; therefore, it is unlikely that second-year birds were present but not observed. Observations of birds banded as juveniles that were resighted in their third year, but not in their second year, were included in the analysis on annual dispersal. The inclusion of these birds increased our sample sizes in the Gulf by 10 individuals (29% of observations) and in sNS by four individuals (33% of observations).

We used linear regression models to determine differences between annual dispersal movements of adults and juveniles in each region (Gulf and sNS). A logarithmic transformation was used to normalize dispersal distances. Linear models were built to examine five possible scenarios: 1) null model (no effect), 2) age class, 3) region, 4) age class + region, and 5) age class + region + age class*region. The Akaike Information Criterion (AIC) and the AIC weight were used to determine the best-fit model (Burnham and Anderson 2002). One bird banded in the Gulf region was resighted in subsequent years in New York and Massachusetts, U.S. (J. Cohen, unpubl. data, Massachusetts Audubon-Coastal Waterbird Program, unpubl. data); this individual plover was not included in this analysis, as dispersal of this distance is clearly an exception that would have skewed typical patterns of dispersal within eastern Canada. All statistical analyses were conducted in R version 2.7.2 (R Development Core Team 2012).

TABLE 2. Comparison of annual dispersal distances of adult and juvenile Piping Plovers in the Gulf and sNS regions of eastern Canada.

Region	Age class	n	Annual dispersal distance (km)	
			Median	Range
Gulf	Adult	134	0.49	0.01–298.55
	Juvenile	35[a]	27.98	0.40–306.33
sNS	Adult	32	4.00	0.01–70.69
	Juvenile	12[b]	18.57	6.52–74.83

[a] Includes 10 individuals that were banded as juveniles and first resighted in their third year.
[b] Includes four individuals that were banded as juveniles and first resighted in their third year.

RESULTS

Of the 887 plovers banded, 251 (28%) were resighted in at least one subsequent year during the study (Table 1). The majority of resighted birds (n = 160, 64%) were only observed once during the study. Return rates were significantly different between age classes in each region (X^2 = 36.501, df = 1,3, $P < 0.001$), with lower than expected return rates for juveniles in both regions (Table 1).

The majority of individuals (229; 92%) returned to the province and region where they were banded (Table 1). Twenty individuals (8%; 11 juveniles and 9 adults) dispersed between provinces in the Gulf region. Of 56 plovers banded in PE, nine (16%) were resighted in other Gulf provinces, and seven of the 20 (35%) interprovincial movements documented throughout the study involved dispersal to PE. Two interprovincial movements were documented for one individual banded in NB, who initially dispersed to PE and then to NS. Although three plovers from other Gulf region provinces dispersed to NL, no birds banded in NL were resighted in other provinces during the study. No plovers were documented dispersing between the Gulf and sNS regions during the study period.

Maximum dispersal distances in the Gulf region were considerably greater (adult: 298.6 km; juvenile: 306.3 km) than those in the sNS region (adult: 70.7 km; juvenile: 74.8 km) (Table 2). Only one adult and two juveniles in the Gulf region, or 1% of all observed individuals, undertook dispersal > 200 km.

Median annual dispersal distances for adults were greater in sNS (4.00 km, range 0.01–74.83) than the Gulf (0.49 km, range 0.01–298.55); however, juvenile dispersal distances were greater in the Gulf region (27.98 km, range: 0.40–306.33) than in sNS (18.57 km, range: 6.52–74.83) (Table 2). The best-fit model for annual dispersal included age class, region, and the interaction term for age and region (Table 3). Average annual dispersal distances were significantly different between age classes ($F_{1,209}$ = 79.158, $P < 0.001$) and regions ($F_{1,209}$ = 8.366, P = 0.004); the interaction effect between age class and region approached significance ($F_{1,209}$ = 3.234, P = 0.074) (Table 3).

Only one individual from eastern Canada was documented short-stopping during this banding study. It was banded as a juvenile in PE and was observed breeding in its second year on Westhampton Beach, New York ~1,025 km from its natal site (J. Cohen, unpubl. data). After failing to produce young in its initial nesting attempt, this individual relocated the following year to Long Beach, Barnstable, Massachusetts, ~250 km away from New York (Massachusetts Audubon-Coastal Waterbird Program, unpubl. data).

DISCUSSION

We found that juvenile Piping Plovers undertook significantly greater movements than adult birds, and juvenile movements in the Gulf region were greater than in sNS. High breeding site fidelity in adult birds has been noted in several other studies (Haig and Oring 1988a, b; Cohen et al. 2006; Catlin 2009; LeDee et al. 2010; Cohen and Gratto-Trevor 2011). Fewer studies have documented trends in site fidelity for juvenile birds; however, juveniles tend to exhibit a lower degree of site fidelity than adults (Haig and Oring 1988a, Catlin 2009, Cohen and Gratto-Trevor 2011). The interaction effect between region and age class suggests that region has an effect on dispersal distance for juveniles, but has less effect on adult birds. Other studies have shown that dispersal of adult Piping Plovers is driven by breeding success of the pair and nearby pairs

TABLE 3. The best-fit model to explain dispersal distance of Piping Plovers included age class (adult and juvenile), region (Gulf and sNS), and the interaction term for age and region. Variables are significant unless otherwise indicated.

Model	K[a]	AIC	ΔAIC	AIC weight
age class + region + age class*region[b]	5	606.8	0.0	0.613
age class + region	4	608.1	1.3	0.325
age class	3	611.4	4.6	0.062
region	3	673.6	66.8	<0.001
null	2	677.6	70.8	<0.001

[a] Number of parameters in the model.
[b] Interaction term ($P = 0.074$).

(Rioux et al. 2011, Roche et al. 2012). Dispersal is also impacted by flooding during the breeding season (Roche et al. 2012) or availability of suitable nesting habitat (Catlin 2009). Dispersal of juvenile birds can be driven by intraspecific competition with older individuals for high quality habitat or inbreeding avoidance (Greenwood and Harvey 1982).

Dispersal distances were shorter for juveniles in sNS than the Gulf, suggesting that juvenile dispersal in sNS may be constrained by the discrete nature of suitable habitat in this region. Beaches in sNS are often shorter and interspersed with unsuitable shoreline habitat, as compared with the longer beaches and more continuous habitat in the Gulf.

Dispersal movements between the Gulf provinces, although infrequent (8% of observations), demonstrate the population connectivity within this region. PE appeared to play a key role in the connectivity of habitat within the Gulf region, likely because of its central geographical location and abundance of suitable habitat.

Maximum dispersal distances of three individuals (1% of observations) in the Gulf region were large enough to extend between beaches where birds were banded in southeast NB and nNS to sNS (~225–230 km). Maximum dispersal distances for adults and juveniles in other North American populations range from 3–1,200 km and 5–1,500 km, respectively (Haig and Oring 1988a, Hillman et al. 2012). The similarity between maximum dispersal distances of adults and juveniles in both regions may reflect the extent of suitable habitat in both regions, with considerably more habitat available in the Gulf region.

Few plovers are observed on the eastern shore of Nova Scotia, therefore no birds were banded or resighted in this area during the study. Given its location on the Atlantic coast, these plovers are thought to be part of the sNS breeding range. Dispersal movements >120 km (5% of those observed) would cover the distance between eastern and northern Nova Scotia, although further research would be needed to fully address population connectivity in this area.

A single individual was documented short-stopping over the course of the study. This represents a dispersal rate between eastern Canada and the U.S. Atlantic coast of 0.4% of resighted individuals. This observation is consistent with a recent analysis of genetic data that suggested that patterns of genetic structure in the *melodus* subspecies may be attributed to low gene flow in the *melodus* subspecies (Miller et al. 2010). Short-stopping is unlikely to have a significant effect on population trends in eastern Canada, and gene flow between Canada and the U.S. is likely minimal (Calvert et al. 2006).

Piping Plovers banded as adults were resighted more frequently than those banded as juveniles. Calvert et al. (2006) documented differences in survival rates for adults and juveniles in the Gulf and sNS regions. Adult survival rates are higher than rates for juveniles in eastern Canada and other populations of Piping Plovers (Larson et al. 2000, Calvert et al. 2006, Catlin 2009, Roche et al. 2010, Cohen and Gratto-Trevor 2011). Some of the differences in the resighting rates in the Gulf region may be driven by the larger dispersal distances of juveniles and the challenges people have in accessing large tracts of suitable habitat in remote areas (especially in northern NB and NL), and therefore researchers visited those places less frequently. The detectability of birds banded as juveniles, particularly as some may not breed in their second year, is likely to be lower than that of adults.

This banding study of Piping Plovers has yielded the first comprehensive information about dispersal movements in eastern Canada and will enable more effective conservation planning for the species. Previous studies have demonstrated

differences in population dynamics (i.e., reproductive success, survival and population growth; Calvert et al. 2006) and habitat use (Flemming et al. 1992, Boyne et al. in press) between the Gulf and sNS regions. The lack of documented dispersal between regions within the study time frame suggests that there is little exchange between the Gulf and sNS regions, providing further evidence of the distinctness of the two regions. The small size of the sNS population, the discrete and discontinuous nature of the habitat, and limited rescue potential from outside populations highlight the vulnerability to extirpation of the sNS population. The information available through various studies in eastern Canada suggests that threats affecting productivity and survival on the breeding and wintering grounds may differ between populations. This may warrant treating the Gulf and sNS as separate populations for management purposes.

Piping Plovers are capable of large-scale dispersal; however, these movements are relatively infrequent. Management of populations throughout the North American range of this species should recognize the importance of scale in conservation. With the limited dispersal and high site fidelity demonstrated by this species, local conservation efforts may not result in regional population increases or the rescue of declining populations elsewhere. Maintaining continuous suitable coastal habitat within the historical range of the species and near currently occupied habitat is necessary to accommodate dispersal in response to changes in habitat quality (Roche et al. 2012) and breeding success (Rioux et al. 2011), and may increase the likelihood of future exchange between populations.

ACKNOWLEDGMENTS

We would like to thank K. Baker, S. Flemming, P. Harris, P. Laporte, L. MacDonnell, A. Marsters, J. McKnight, C. Rock, F. Shaffer, J. Stewart, P. Thomas, Eastern Canada Piping Plover Recovery Team and Working Group, Attention FragÎles, Bird Studies Canada, Canadian Parks and Wilderness Society, Irving Eco-Centre – La Dune de Bouctouche, Island Nature Trust, Marine and Mountain Zone Corporation, Nature NB, New Brunswick Nature Trust, Nova Scotia Bird Society, Parks Canada Agency (Kejimkujik, Kouchibouguac and Prince Edward Island National Parks of Canada) and Piper Project/Projet siffleur for their contributions to this research project. C. Gjerdrum and G. J. Robertson kindly provided assistance with data analysis, and M. Elliott prepared the map included in this paper. Helpful comments on a draft were provided by S. Abbott, C. L. Gratto-Trevor, F. Shaffer and two anonymous reviewers. This work was conducted with financial support from the Species at Risk program of the Canadian Wildlife Service, Atlantic and Québec regions.

LITERATURE CITED

Amirault, D. L., F. Shaffer, and J. Stewart. 2006a. Eastern Canada Piping Plover banding summary. Technical report series no. 458. Canadian Wildlife Service, Atlantic Region and Québec Region, Canada.

Amirault, D. L., J. McKnight, F. Shaffer, K. Baker, L. MacDonnell, and P. Thomas. 2006b. Novel anodized aluminum bands cause leg injuries in Piping Plovers. Journal of Field Ornithology 77:18–20.

Boyne, A. W., D. L. Amirault-Langlais, and A. J. McCue. In Press. Characteristics of Piping Plover nesting habitat in the Canadian Maritime Provinces. Northeastern Naturalist.

Burnham, K. and D. Anderson. 2002. Model selection and multi-model interference: a practical information-theoretic approach. Springer, New York, USA.

Cairns, W. E. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bulletin 94:531–545.

Calvert, A. M., D. L. Amirault, F. Shaffer, R. Elliot, A. Hanson, J. McKight, and P. D. Taylor. 2006. Population assessment of an endangered shorebird: the Piping Plover (*Charadrius melodus melodus*) in eastern Canada. Avian Conservation and Ecology – Écologie et conservation des oiseaux 1: www/ace-eco.org/vol1/iss3/art4/ (accessed 8 Nov 2012).

Catlin, D. H. 2009. Population dynamics of Piping Plovers (*Charadrius melodus*) on the Missouri River. Ph.D thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Cohen, J. B. and C. Gratto-Trevor. 2011. Survival, site fidelity, and the population dynamics of Piping Plovers in Saskatchewan. Journal of Field Ornithology 82:379–394.

Cohen, J. B., J. D. Fraser, and D. H. Catlin. 2006. Survival and site fidelity of Piping Plovers on Long Island, New York. Journal of Field Ornithology 77:409–417.

Drake, K. R., J. E. Thompson, K. L. Drake, and C. Zonick. 2001. Movements, habitat use and survival of nonbreeding Piping Plovers. Condor 103:259–267.

Elliott-Smith, E., S. M. Haig, and B. M. Powers. 2009. Data from the 2006 International Piping Plover Census. U.S. Geological Survey Data Series 426. http://pubs.usgs.gov/ds/426/ (accessed 14 Jan 2013).

Environment Canada. 2012. Recovery strategy for the Piping Plover (*Charadrius melodus melodus*) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada. Ottawa, Canada.

Flemming, S. P., R. D. Chiasson, and P. J. Austin-Smith. 1992. Piping Plover nest site selection in New Brunswick and Nova Scotia. Journal of Wildlife Management 56:578–583.

Goossen, J. P. and D. L. Amirault-Langlais (Editors). 2010. The 2006 International Piping Plover Census in Canada. Technical Report Series No. 490. Canadian Wildlife Service, Prairie and Northern Region and Atlantic Region, Canada.

GRATTO-TREVOR, C., D. AMIRAULT-LANGLAIS, D. CATLIN, F. CUTHBERT, J. FRASER, S. MADDOCK, E. ROCHE, AND F. SHAFFER. 2012. Connectivity in Piping Plovers: do breeding populations have distinct winter distributions? Journal of Wildlife Management 76:348–355.

GRATTO-TREVOR, C. L. AND S. ABBOTT. 2011. Conservation of Piping Plover (*Charadrius melodus*) in North America: science, successes, and challenges. Canadian Journal of Zoology 89:401–418.

GREENWOOD, P. J. AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

HAIG, S. M. AND E. ELLIOT-SMITH. 2004. Piping Plover (*Charadrius melodus*). The birds of North America. Number 002.

HAIG, S. M. AND L. W. ORING. 1988a. Distribution and dispersal in the Piping Plover. Auk 105:630–638.

HAIG, S. M. AND L. W. ORING. 1988b. Mate, site and territory fidelity in Piping Plovers. Auk 105:268–277.

HAIG, S. M., C. L. FERLAND, F. J. CUTHBERT, J. DINGLEDINE, J. P. GOOSSEN, A. HECHT, AND N. MCPHILLIPS. 2005. A complete species census and evidence for regional declines in Piping Plovers. Journal of Wildlife Management 69:160–173.

HECHT, A. AND S. M. MELVIN. 2009. Population trends of Atlantic coast Piping Plovers, 1986–2006. Waterbirds 32:64–72.

HILLMAN, M. D., S. M. KARPANTY, J. D. FRASER, F. J. CUTHBERT, J. M. ALTMAN, T. E. BORNEMAN, AND A. DEROSE-WILSON. 2012. Evidence for long-distance dispersal and successful interpopulation breeding of the endangered Piping Plover. Waterbirds 35:642–644.

KNETTER, J. M., R. K. MURPHY, AND R. S. LUTZ. 2001. Initial movements of juvenile Piping Plovers, *Charadrius melodus*, from natal sites in northwestern North Dakota. Canadian Field Naturalist 115:352–353.

LARSON, M. A., M. R. RYAN, AND B. G. ROOT. 2000. Piping Plover survival in the Great Plains: and updated analysis. Journal of Field Ornithology 71:721–729.

LEDEE, O. E., T. W. ARNOLD, E. A. ROCHE, AND F. J. CUTHBERT. 2010. Use of breeding and nonbreeding encounters to estimate survival and breeding-site fidelity of the Piping Plover at the Great Lakes. Condor 112:647–643.

MILLER, M. P., S. M. HAIG, C. L. GRATTO-TREVOR, AND T. D. MULLINS. 2010. Subspecies Status and Population Genetic Structure in Piping Plover (*Charadrius melodus*). Auk 127:57–71.

R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RIOUX, S., D. L. AMIRAULT-LANGLAIS, AND F. SHAFFER. 2011. Piping Plovers make decisions regarding dispersal based on personal and public information in a variable coastal ecosystem. Journal of Field Ornithology 82:32–43.

ROCHE, E. A., J. B. COHEN, D. H. CATLIN, D. L. AMIRAULT-LANGLAIS, F. J. CUTHBERT, C. L. GRATTO-TREVOR, J. FELIO, AND J. D. FRASER. 2010. Range-wide Piping Plover survival: correlated patterns and temporal declines. Journal of Wildlife Management 74:1784–1791.

ROCHE, E. A., C. L. GRATTO-TREVOR, J. P. GOOSSEN, AND C. L. WHITE. 2012. Flooding affects dispersal decisions in Piping Plovers (*Charadrius melodus*) in prairie Canada. Auk 129:296–306.

U.S. FISH AND WILDLIFE SERVICE (USFWS). 1986. Endangered and threatened wildlife and plants: Determination of endangered and threatened status for the Piping Plover – final rule. Federal Registry 50:50726–50734.

WELLER, M. W. 1957. An automatic nest-trap for waterfowl. Journal of Wildlife Management 21:456–458.

WILCOX, L. 1959. A twenty year banding study of the Piping Plover. Auk 76:129–152.

The Wilson Journal of Ornithology 126(2):359–366, 2014

Modeling Greater Roadrunners' (*Geococcyx californianus*) Habitat Use in West Texas

Andrea E. Montalvo,[1,3] Dean Ransom, Jr.,[1,2] and Roel R. Lopez[1]

ABSTRACT.—We studied Greater Roadrunners' (*Geococcyx californianus*) habitat use during spring and summer of 2011 in the Red Rolling Plains of west Texas. We captured 10 roadrunners (one male and nine females) and fitted each with a 10-g backpack style radio-transmitter. Roadrunners were relocated 2–4 times per week from February–August. We used these data to build a logistic regression model to better understand the vegetative and topographic features important to roadrunners during the nesting season. The initial data set consisted of 30 random and 30 used locations. The best model showed both percent rock and percent litter to be

[1] Department of Wildlife and Fishery Sciences, Texas A&M University, 2258 TAMU, College Station, TX 77843, USA.
[2] Current address: Clifton, TX 76634, USA.
[3] Corresponding author; e-mail: aem595@tamu.edu

higher at used locations and correctly classified 88% of the sites. Evaluation of the model with an additional 30 random and 30 used locations maintained significance of both the model and variables and correctly classified 83% of sites. Both variables were associated with the location's mesa ridge slopes. Litter dominated locations under shrubs on the ridge tops and slopes and likely provided security from predators, nest sites, and relief from extreme summer temperatures. Percent rock cover characterized locations on ridge tops and slopes which provided perch sites, travel lanes, and foraging sites where the roadrunners could find basking prey. *Received 26 June 2013. Accepted 24 December 2013.*

Key words: *Geococcyx californianus*, habitat use, logistic regression, model, telemetry, Texas.

Greater Roadrunners (*Geococcyx californianus*) are iconic terrestrial and predatory birds unique to North American rangelands and open woodlands (Hughes 1996, Maxon 2005). To date, Greater Roadrunners have been poorly studied despite their familiarity and visibility. Early research on roadrunner ecology consisted of observational descriptive accounts of range size and movements (Ohmart 1973, Folse 1974, Meinzer 1993, Hughes 1996, Maxon 2005, Payne et al. 2005, Kelley et al. 2011).

Recently, Kelley et al. (2011) employed a more modern approach using radio-telemetry to quantify home range, survival and habitat selection of roadrunners in north Texas. The near lack of information regarding habitat selection is unfortunate given that habitat loss, conversion, and fragmentation is rapidly occurring in much of the species' range. Where large tracts of native range still occur, land management practices such as brush management to improve livestock forage pose threats to nesting sites and thermal refugia (Rylander 1972, Vehrencamp 1982, Cook 1997).

In recent research efforts avian ecologists have utilized a fine scale approach, either organism-based or attribute-based (e.g., nest site, foraging site), in a use-availability framework to quantify and model micro-site habitat or resource selection by a variety of birds (Johnson and Guthery 1988, Kopp et al. 1998, Rodrigues 1994, Nolte and Fulbright 1996, Sutter and Ritchison 2005, Maccarone and Brzorad 2005). Kelley et al. (2011) and Montalvo (2012) have shown roadrunners' preference for woody cover at landscape and home range spatial scales; these two studies found no selection or avoidance for any cover type at third order scales (e.g., within home range; Johnson 1980).

In our study, we sought to quantify and model micro-habitat selection by roadrunners occupying semi-arid range-land in west Texas. To do this, we constructed a model using habitat data measured at both triangulated locations of roadrunners and random locations. To that end, our study is unique in that it is the first of its kind to address knowledge gaps that will be important in conservation and management of roadrunners.

METHODS

We collected data from February–August 2011 on the 1902-ha Rolling Plains Quail Research Ranch (RPQRR; 32° 02′ 16″ N, 100° 32′ 50″ E) in the Rolling Plains ecological region (Gould 1975) in Fisher County, Texas. The RPQRR contained pockets of mixed grass prairie, Conservation Reserve Program (CRP) fields, food plots, and dense stands of honey mesquite (*Prosopis glandulosa*), Havard oak (*Quercus havardii*), and Pinchot's juniper (*Juniperus pinchotii*).

An unbroken series of mesa-ridge slopes was a prominent topographical feature that spanned the entire north-south axis of the RPQRR (Fig. 1). These geologic uplifts were characterized by shallow, gravelly, reddish brown soils and quartizitic pebbles over conglomerate rock or sandstone (U.S. Geological Survey 1972). Ridge slopes were vegetated by large dense mottes of shrubs while ridge tops supported small, sparse patches of shrubs and mixed grasses. Land management practices on RPQRR included prescribed burns, mechanical shrub control, as well as aerial and ground application of herbicide. Land development on the study site consisted of gravel and dirt roads, barbed wire fences, water troughs, and electrical poles. The surrounding private land use included natural pastures, CRP fields, and cotton fields left fallow after harvest.

We captured roadrunners using two methods. The first method was a modified bal-chatri trap (Berger and Mueller 1959, Vilella and Hengstenberg 2006, Lake et al. 2002) that consisted of a caged mouse (*Mus musculus*) surrounded by monofilament nooses on plywood boards that were nailed into the ground. These adjustments were implemented to address the unique ground-level hunting style of roadrunners (Kelley et al. 2011). The second technique was a box trap with a caged mouse in the back as bait (Vehrencamp and Halpenny 1981, Kelley et al. 2011, Bub 1991).

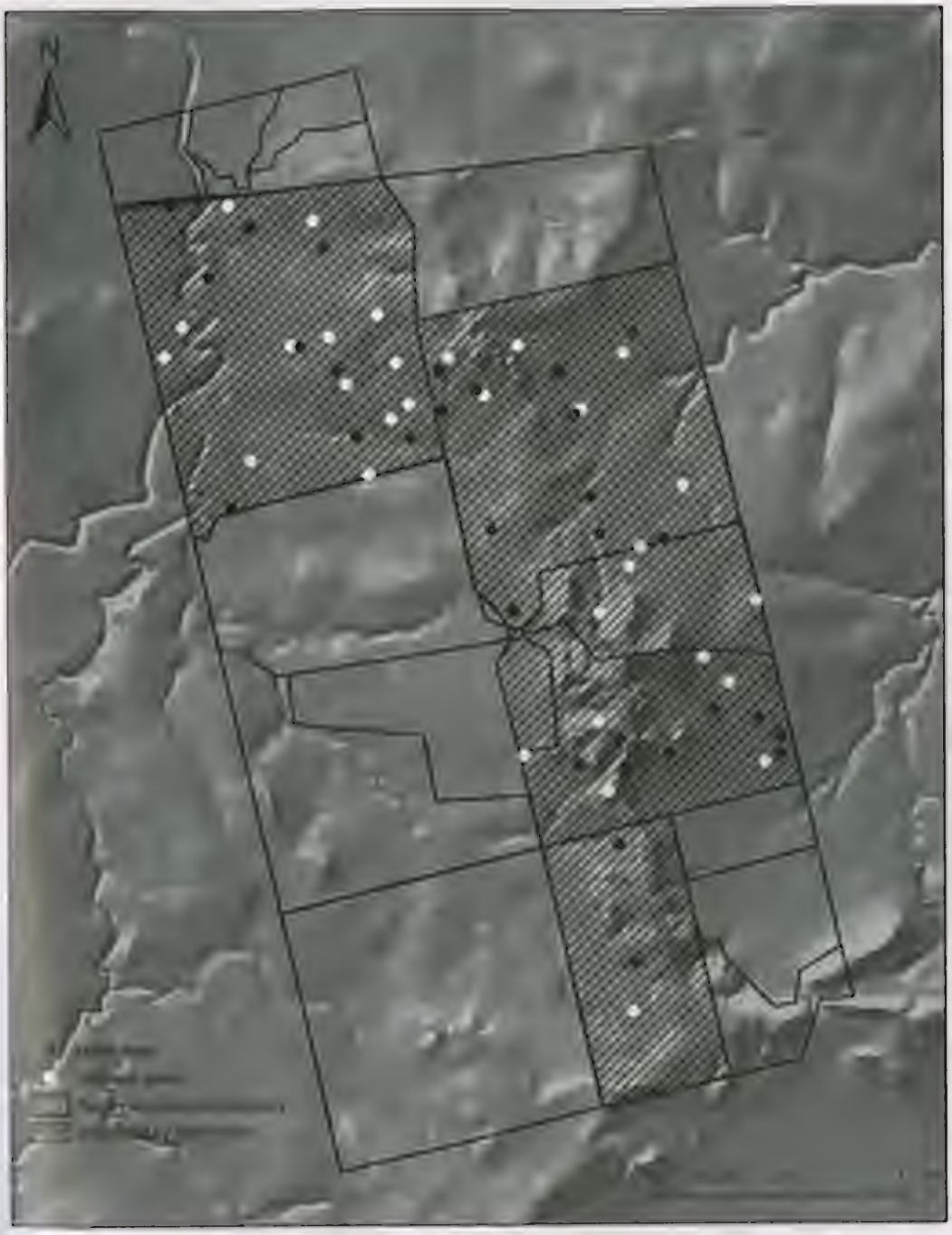


FIG. 1. Roadrunners use mostly the pastures indicated with stripes in the hill-shaded study site. The mesa uplifts used heavily by all birds can be seen on the eastern portion of the ranch running from north to south. Black dots represent the random points used during model selection and white dots were random locations used during validation.

After capture, we removed a small number of downy feathers for sex verification through PCR DNA analysis following the methods of Santamaria et al. (2010). Birds were then fitted with a 10-g back-pack style radio-transmitter and immediately released at the capture site. Our research protocols were approved by the Texas A&M University Institutional Animal Care and Use

TABLE 1. Distribution of 30 random locations amongst the 10 roadrunners used for development of the model and 30 locations used for model validation.

Roadrunner	Model locations	Validation locations
A	-	2
B	8	5
C	8	7
D	2	-
E	-	1
F	-	-
G	8	8
H	-	4
I	2	-
J	2	3

Committee (TAMU AUP# 2009-61), Texas Parks and Wildlife Scientific Permit SPR-0602-219, and USFWS scientific permit MB155578-1.

We relocated roadrunners 2–4 times per week via triangulation of compass bearings from 3–5 positions. Locations were calculated with the program LOCATE III (Nams 2006) utilizing the maximum likelihood estimator and estimated standard deviation settings. We considered a location to be acceptable when the location error ellipse was <1 ha. This was used as a threshold from which to gauge the strength of a triangulation (Saltz and Alkon 1985). When triangulation errors are large compared to habitat patch size, precision suffers and bias is introduced as there is an increased likelihood of type II error when determining habitat preference (White and Garrott 1986, Nams 1989, Saltz 1994).

We modeled micro-habitat selection using 30 sample points each for used and random locations. Roadrunner locations were pooled and randomly selected (Table 1). Random locations were determined using ArcMap's random location generator (ESRI 2009), and stratified to consider only the portions of the ranch in which roadrunners were known to inhabit (Fig. 1). We treated each used and random point as the center of a circular patch with a 10-m radius in which we measured vegetation and ground cover attributes. We used four 10-m radii in the four compass directions emanating from the point as line intercepts. We measured brush canopy cover using the line intercept method of Canfield (1941). We estimated brush density within the patch by dividing the total number of shrubs by the area sampled (Density = $n/2\pi[10]^2$).

We used a Robel pole (Robel et al. 1970) to estimate visual obstruction and the disc of vulnerability. The disc of vulnerability is the distance at which a specified height on the Robel pole is totally obscured (Kopp et al. 1998); the disc measures the distance at which an organism might be visible to ground dwelling predators. We used a height of 30-cm corresponding to the standing height of a roadrunner and measured the distance at which the 30-m strata was totally obscured using a laser rangefinder.

We then used a 20 × 50-cm sampling frame at five points (2, 4, 6, 8, and 10-m) along four line transects in the compass directions to visually estimate percent grass, forb, litter, rock, and bare ground exposure. Finally, the nearest edge type was recorded (i.e., game trail, road, ridge, brush line, contour, and disked strip). All vegetative measurements were repeated in the same manner at both used and random locations (Ransom et al. 2008). We calculated means and 95% confidence intervals (CI) for all habitat variables and tested the data for a normal distribution. Means of differences in random and telemetry locations for all continuous habitat data were then determined using the non-parametric Wilcoxon signed-rank test (Ransom et al. 2008).

A nominal logistic regression model was developed to try to correctly classify a location as random (model = 0) or used location (model = 1). Regression analysis was run on full, reduced, and constant only models and the strongest model was chosen based on the goodness-of-fit test, lack of fit test, AIC*c*, and the area under the receiver operating characteristics curve (AUC). The receiver operating characteristic curve is used to demonstrate a binary model's ability to correctly distinguish between two groups (i.e., male or female roadrunners). In this case, the AUC is used to compare the ability of multiple models to discriminate between the males and females. An AUC ranges between 0–1, so that an AUC = 0.5 indicates the model is no better than random at assigning gender while an AUC = 1.0 perfectly distinguishes between male and female roadrunners. The 95% CI for the AUC was calculated using a bootstrap method with 1,000 iterations. Once a model was considered, we tested the variables for interactions with a Spearman's rank correlation coefficient and pairs of variables that were found to be highly correlated had one variable removed before any further consideration. Odds ratios for the variables in the chosen model were then reported with their confidence intervals.

We validated the model with an independent data set of an additional 30 samples for both used

TABLE 2. Comparison of continuous means of habitat data at used locations versus random locations in west Texas.

Variable (n = 60)	Random mean (CI)	Location mean (CI)	Wilcoxon signed-rank
Distance to edge	16.18 (8.02, 24.34)	8.01 (4.55, 11.50)	$T = 67.5$, $P = 0.050$
Visual obstruction	1.10 (0.71, 1.49)	1.23 (0.73, 1.72)	$T = -103.5$, $P = 0.031$
Disc of vulnerability	27.27 (20.06, 34.48)	18.73 (15.72, 21.73)	$T = 111.5$, $P = 0.019$
Brush CC	0.10 (0.04, 0.15)	0.29 (0.21, 0.36)	$T = -213.5$, $P < 0.0001$
Brush density	0.13 (0.10, 0.17)	0.16 (0.13, 0.18)	$T = -77.5$, $P = 0.112$
% Bare ground	30.25 (22.13, 38.37)	13.76 (8.81, 18.71)	$T = 165.5$, $P = 0.0002$
% Rock	4.16 (1.34, 6.97)	21.88 (15.02, 28.73)	$T = -228.5$, $P < 0.0001$
% Litter	32.04 (24.95, 39.13)	42.13 (34.60, 49.67)	$T = -124.5$, $P = 0.008$
% Grass	31.79 (23.33, 40.25)	21.23 (16.78, 25.68)	$T = 96.5$, $P = 0.045$
% Forbs	1.94 (1.03, 2.85)	0.63 (−0.14, 1.39)	$T = 101.0$, $P = 0.0344$

and random points chosen in the same manner. All data analysis were performed using JMP 9 (SAS Institute 2007) and ArcGIS 9.3.1 (ESRI 2009) with a significance level of $\alpha = 0.05$.

RESULTS

Ten roadrunners (one male, nine females) were caught over the course of the study. These roadrunners were relocated a total of 437 times excluding the two relocations with the largest triangulation error polygons. The average error polygon was 0.64 ha (CI = 0.24, 1.05).

The statistics for continuous variables measured all showed a significant difference between actual and random locations except brush density (Table 2). Similarly, all categorical statistics were significantly different between actual and random sites except creek, brush line, contour, and disk strip edge types as their low occurrence made probability testing unreliable (Table 3).

Model exploration resulted in six potential models (Table 4). While model (M_2) had the highest AUC and one of the lowest AICc, not all of the parameter estimates were significant. The same was true for models (M_3), (M_4), and (M_6). The two remaining models, (M_1) and (M_5), had significant parameter estimates, significant whole model tests, and neither showed a lack of fit. (M_1) was chosen as the top model over (M_5) because of both its lower AICc and higher AUC (CI = 0.78, 0.95). Model (M_1) contained percent rock (R; $P = 0.0001$), percent litter (L; $P = 0.0052$), and intercept ($P = 0.0006$). The odds ratio of actual versus random locations for rock was 1912.524 (CI = 64.24, 178609.6) and litter was 64.478 (CI = 4.256, 1603.542). Litter and Rock were not found to be significantly correlated ($r_s = -0.0966$, $P = 0.46$).

Model validation with an additional 30 random and 30 used locations ($n = 60$) similarly found rock ($P = 0.008$), litter ($P = 0.0214$), and the intercept ($P = 0.007$) to be significant. There was no lack of fit ($\chi^2 = 67.53$, $P = 0.14$), the whole model test was significant ($\chi^2 = 12.87$, $P = 0.002$), and the AUC measured 0.83 (CI = 0.64, 0.89).

TABLE 3. Comparison of categorical habitat data proportions at used locations versus random locations in west Texas.

Variable (n = 60)	Random	Actual	Pearson's χ^2
Ridge	0.13	0.70	$\chi^2 = 45.87$, $P < 0.0001$
Edge type			
Road	0.53	0.13	$\chi^2 = 0.53$, $P < 0.0001$
Game trails	0.17	0.47	$\chi^2 = 10.85$, $P = 0.001$
Ridge	0.03	0.27	$\chi^2 = 8.35$, $P = 0.004$
Creek[a]	0.00	0.10	
Brush line[a]	0.00	0.03	
Contour[a]	0.20	0.00	
Disk strip[a]	0.07	0.00	

[a] Low occurrence at random and actual sites makes probability testing unreliable.

DISCUSSION

Vegetation structure at roadrunner locations differed from that at random locations in all variables measured except brush density. Brush density at both used and random locations were similar and uniformly low, averaging <1 plant/ha. The remaining nine variables appear to reflect the roadrunners' foraging needs as well as the need to minimize vulnerability to predators. Roadrunner locations were closer to edges (Tables 2, 3), had lower percent grass cover, forb, and bare ground, but higher percent cover of rock. Such locations may facilitate the search for small reptiles and arachnids, as well as large orthopterans. Areas of bare rock, especially on ridge-slope mesas, provide ideal basking sites for both snakes and

TABLE 4. Top models including the variables percent rock (R), percent liter (L), brush density (BD), and brush canopy cover (CC) as well as their associated whole model test results, lack of fit test results, AIC*c*, and AUC.

Models ($n = 60$)	All parameter estimates significant?	Whole model test	Lack of fit	AIC*c*	AUC
$(M_1) = 3.36 - 0.12(R) - 0.05(L)$	All significant	$\chi^2 = 31.08$ $P < 0.0001$	$\chi^2 = 52.10$ $P = 0.659$	58.53	0.88
$(M_2) = -2.57 - 7.29(BD) + 5.46(CC) + 0.11(R) + 0.04(L)$	Only rock and intercept	$\chi^2 = 35.49$ $P < 0.0001$	$\chi^2 = 47.68$ $P = 0.748$	58.80	0.90
$(M_3) = -3.22 - 1.59(BD) + 0.12(R) + 0.05(L)$	All significant except brush density	$\chi^2 = 31.22$ $P < 0.0001$	$\chi^2 = 51.96$ $P = 0.629$	60.69	0.88
$(M_4) = -3.25 + 3.50(CC) + 0.10(R) + 0.04(L)$	Only rock and intercept	$\chi^2 = 33.59$ $P < 0.0001$	$\chi^2 = 49.59$ $P = 0.715$	58.32	0.89
$(M_5) = -1.09 + 0.10(R)$	All significant	$\chi^2 = 21.51$ $P < 0.0001$	$\chi^2 = 33.33$ $P = 0.500$	65.88	0.82
$(M_6) = -0.99 + 0.27(L)$	None significant	$\chi^2 = 3.96$ $P = 0.047$	$\chi^2 = 76.45$ $P = 0.030$	83.43	0.63

lizards and den sites for rodents, all of which are important food items in the diet of roadrunners. Roadrunners also selected sites that provided greater concealment than random locations, greater percent brush canopy cover, and higher visual obstruction values. These vegetation attributes would have provided screening and escape cover from ground predators such as coyotes (*Canis latrans*), and aerial predators such as Cooper's hawks (*Accipiter cooperii*) and Red-tailed Hawks (*Buteo jamaicensis*; Maxon 2005).

Our results are difficult to compare to past literature because of both the lack of available information and differences in methodology. Kelley et al.'s (2011) more recent roadrunner study found roadrunners preferred areas with shrubs and canopy cover and avoided areas with greater percentages of grass and bare ground. Folse and Arnold's (1978) earlier land use study found roadrunners associated with brush but also heavily used grasslands for foraging. Folse's results relied on opportunistic resightings, therefore likely biasing results towards the more visible habitats. Meinzer's (1993) observations in north-central Texas, in contrast, detected no preferential use of habitat.

Our logistic model (M_1) indicated that percent rock and litter cover were important in distinguishing between used and random locations. We believed that this is a result of the disproportionate use of mesa-ridges (Table 3). These geologic uplifts were largely comprised of rock substrates with shallow soil, scattered mottes of shrubs, and sparse herbaceous cover. Thus, it was not surprising that percent rock cover would be important. Locations near or under shrub mottes contained high percentages of leaf litter on the ground; shrub mottes were the main source of shade, and with a relatively open ground cover, roadrunners could maximize the cooling effects of upslope breezes. Depending on the weather, shrubs on the ridge top also offered protection from prevailing winds and one of the few areas of shade for thermoregulation (Rylander 1972, Johnson and Guthery 1988, Wolf and Walsberg 1996). Roadrunners use shade as cooler microclimates to economize their energy resources. In these cooler areas, roadrunners will raise their internal temperature to maximize heat loss and minimize evaporative water loss (Rylander 1972, Cook 1997). Finally, shrubs are the primary nesting substrate for roadrunners (Ohmart 1972, Folse 1974, Meinzer 1993, Hughes 1996, Payne et al. 2005), as well as provide perch sites for calling and visual detection of prey.

We believe that litter likely offered little direct benefit to roadrunners, beyond habitat for small prey, and may be an artifact of the location being associated with mesa-slope shrub cover. Percent rock cover was more directly related to the roadrunners visual detection of prey. Although these two variables were unexpected as model predictors, they both allude to the importance of ridge top and ridge slopes where most roadrunners were encountered during the course of this study.

Our logistic model performs with a high degree of accuracy as demonstrated by the model's AUC. We must note however, that our study was conducted in one of the most severe droughts since the 1950s which may have affected our model performance. We did not detect any nesting activity among our sample of birds, which we also

attribute to the drought. Therefore, our model may not be realistic in years when weather conditions are more amendable to nesting activity. Our model was based on data collected at only one study site, limiting our inference ability. Additionally, though our data indicates microhabitat selection preferences, the inherent error associated with telemetry, though small, reflects the general vicinity around a true roadrunner location. However, our study is the first of its kind and as such represents an initial contribution to understanding micro-habitat selection and a foundation for future research.

ACKNOWLEDGMENTS

This work was completed with the support of the Louis Stokes Alliance for Minority Participation's Bridge to Doctorate Fellowship. The Rolling Plains Quail Research Ranch provided room and board, and access to the ranch as a study site. The Department of Wildlife and Fisheries Sciences provided office space and computer access. Additionally, we are grateful for the advice of R. A. Feagin, A. R. Rodgers, L. M. LaCoste, B. A. Koennecke, and R. N. Perkins.

LITERATURE CITED

BERGER, D. D. AND H. C. MUELLER. 1959. The bal-chatri: a trap for the birds of prey. Bird-Banding 30:18–26.

BUB, H. 1991. Bird trapping and bird banding: a handbook for trapping methods all over the world, Cornell University Press, Ithaca, New York, USA.

CANFIELD, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.

COOK, W. E. 1997. Avian desert predators (adaptations of desert organisms), Springer, New York, USA.

ESRI. 2009. ArcGIS. ESRI, Redlands, California, USA.

FOLSE, L. J., JR. 1974. Population ecology of roadrunners (*Geococcyx californianus*) in south Texas. Wildlife Science, Texas A&M Univeristy, College Station, USA.

FOLSE, L. J., JR. AND K. A. ARNOLD. 1978. Population ecology of roadrunners (*Geococcyx californianus*) in south Texas. Southwestern Naturalist 23:1–27.

GOULD, F. W. 1975. Texas plants: a checklist and ecological summary, Texas Agricultural Experiment Station, USA.

HUGHES, J. M. 1996. Greater Roadrunner (*Geococcyx californianus*). The birds of North America. Number 244.

JOHNSON, D. B. AND F. S. GUTHERY. 1988. Loafing coverts used by Northern Bobwhites in subtropical environments. Journal of Wildlife Management 52: 464–469.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

KELLEY, S. W., J. D. RANSOM, J. A. BUTCHER, G. G. SCHULZ, B. W. SURBER, W. E. PINCHAK, C. A. SANTAMARIA, AND L. A. HURTADO. 2011. Home range dynamics, habitat selection, and survival of Greater Roadrunners. Journal of Field Ornithology 82:165–174.

KOPP, S. D., F. S. GUTHERY, N. D. FORRESTER, AND W. E. COHEN. 1998. Habitat selection modeling for Northern Bobwhites on subtropical rangeland. Journal of Wildlife Management 62:884–895.

LAKE, L. A., D. A. BUEHLER, AND A. E. HOUSTON. 2002. Cooper's Hawk non-breeding habitat use and home range in southwestern Tennessee. Proceedings of the Annual Conference of the Southeastern Association Fish & Wildlife Agencies (SEAFWA), Tallahassee. 56:229–238.

MACCARONE, A. D. AND J. N. BRZORAD. 2005. Foraging microhabitat selection by wading birds in a tidal estuary, with implications for conservation. Waterbirds 28:383–391.

MAXON, M. A. 2005. The real roadrunner, University of Oklahoma Press, Norman, USA.

MEINZER, W. 1993. The roadrunner. Tenth Anniversary Edition, Texas Tech University Press, Lubbock, USA.

MONTALVO, A. 2012. Nesting range, spatial use, habitat selection and sex identification of the Greater Raodrunner (*Geococcyx californianus*). Master of Science, Texas A&M University, College Station, USA.

NAMS, V. O. 1989. Effects of radiotelemetry error on sample size and bias when testing for habitat selection. Canadian Journal of Zoology 67:1631–1636.

NAMS, V. O. 2006. Locate III user's guide. Pacer Computer Sofware, Tatamagouche, Nova Scotia, Canada.

NOLTE, K. R. AND T. E. FULBRIGHT. 1996. Nesting ecology of Scissor-Tailed Flycatchers in south Texas. Wilson Bulletin 108:302–316.

OHMART, R. D. 1972. Physiological and ecological observations concerning the salt-secreting nasal glands of the roadrunner. Comparative Biochemistry and Physiology Part A: Physiology 43:311–316.

OHMART, R. D. 1973. Observations on the breeding adaptations of the roadrunner. Condor 75:140–149.

PAYNE, R. B., M. D. SORENSEN, K. KLITZ, AND J. MEGAHAN. 2005. The cuckoos: bird families of the world Oxford University Press, New York, USA.

RANSOM, D., R. R. LOPEZ, G. G. SCHULZ, AND J. S. WAGNER. 2008. Northern Bobwhite habitat selection in relation to brush management in the rolling plains of Texas. Western North American Naturalist 68:186–193.

ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

RODRIGUES, R. 1994. Microhabitat variables influencing nest-site selection by tundra birds. Ecological Applications 4:110–116.

RYLANDER, M. K. 1972. Winter dormitory of the roadrunner, *Geococcyx californicus*, in west Texas. Auk 89:896.

SALTZ, D. 1994. Reporting error measures in radio location by triangulation: a review. Journal of Wildlife Management 58:181–184.

SALTZ, D. AND P. U. ALKON. 1985. A simple computer-aided method for estimating radio-location error. Journal of Wildlife Management 49:664–668.

SANTAMARIA, C. A., S. KELLEY, G. G. SCHULZ, D. RANSOM, AND L. A. HURTADO. 2010. Polymerase chain reaction-based sex identification in the Greater Roadrunner. Journal of Wildlife Management 74:1395–1399.

SAS INSTITUTE. 2007. SAS Institute Inc., Cary, North Carolina, USA.

U.S. GEOLOGICAL SURVEY. 1972. Bull creek quadrangel, Texas - Fisher Co., 1969 : 7.5 min series (topographic). U.S. Geological Survey Denver, Colorado, USA.

SUTTER, B. AND G. RITCHISON. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. Journal of Field Ornithology 76:345–351.

VEHRENCAMP, S. L. 1982. Body temperatures of incubating versus non-incubating roadrunners. Condor 84:203–207.

VEHRENCAMP, S. L. AND L. HALPENNY. 1981. Capture and radio-transmitter attachment techniques for roadrunners. North American Bird Bander 6:128–132.

VILELLA, F. J. AND D. W. HENGSTENBERG. 2006. Broad-winged Hawk (*Buteo platypterus brunnescens*) movements and habitat use in a moist limestone forest of Puerto Rico. Ornitologia Neotropical 17:563–579.

WHITE, G. C. AND R. A. GARROTT. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. Journal of Wildlife Management 50:509–513.

WOLF, B. O. AND G. E. WALSBERG. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. Ecology 77:2228–2236.

The Wilson Journal of Ornithology 126(2):366–369, 2014

Light Pollution Allows the Northern Mockingbird (*Mimus polyglottos*) to Feed Nestlings After Dark

Christine M. Stracey,[1,2,3] Brady Wynn,[1] and Scott K. Robinson[1]

ABSTRACT.—We investigated whether Northern Mockingbirds (*Mimus polyglottos*) alter their nocturnal foraging behavior in areas with artificial light at night. We observed mockingbirds after sunset at six study sites that varied in levels of artificial light. We hypothesized that birds at the parking lot and residential sites would feed their nestlings later at night because of light pollution. The average time past sunset that birds across all sites continued to feed nestlings was positively correlated with average light level around the nest. Mockingbirds in the parking lot fed their nestlings ~15 mins later than those in the other sites, suggesting that this abundant urban species can exploit light pollution. *Received 9 July 2013. Accepted 13 February 2014.*

Key words: ecological light pollution, nestling feeding, Northern Mockingbird, urban ecology.

Urbanization significantly contributes to ecological light pollution, and harmful effects have been documented in a wide range of taxa (reviewed in Longcore and Rich 2004, Gaston et al. 2013). However, some organisms exploit the night light niche (Garber 1978) by consuming organisms that are attracted to artificial lighting (e.g., Lebbin et al. 2007). The ability to adjust behaviorally to light pollution therefore may help some species successfully inhabit urban environments.

The Northern Mockingbird (*Mimus polyglottos*) is primarily insectivorous when breeding and occurs in a variety of habitats that vary in artificial light levels. Mockingbirds are more likely to sing at night in the presence of artificial light (Derrickson 1988) and have been recorded foraging after sunset (Derrickson and Breitwisch 1992), possibly because insects are attracted to and may be easier to see at night in habitats with artificial light (Frank 1988). In this study, we observed mockingbirds in a parking lot, two residential neighborhoods, a cattle pasture, and a wildlife preserve after sunset to determine if nestling-feeding behavior varied with light level. We hypothesized that artificial lights would create conditions bright enough to allow mockingbirds in the parking lot and residential neighborhoods to feed their nestlings later into the night.

[1] Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, FL 32611 USA.
[2] Current address: Biology Department, Westminster College, Salt Lake City, UT 84105, USA.
[3] Corresponding author;
e-mail: cstracey@westminstercollege.edu

METHODS

Study sites were within 50 km of Gainesville, FL (population 124,354; 2010.census.gov/2010census/) and were between 2.7 and 52.9 km from each other. The sites differed in average proportion of ground cover consisting of pavement and buildings (Le Gros et al. 2011) and each site was embedded within a larger area of the same land use.

We located mockingbird nests at each site during the 2008–2009 breeding seasons (Mar–Jul). We placed video cameras on a random subset of nests in the residential neighborhoods, pasture, and wildlife preserve (see Stracey 2011 for details on camera setup). No cameras were placed in the parking lot because of risk of theft. We determined hatching date by checking nests every 1–3 days in the parking lot and used video footage at the other sites. We conducted nestling feeding observations starting at sunset and lasting 1 hr after sunset or 20 mins past the last feeding trip if the birds were still feeding after the 1-hr period. We expect to see at least one feeding trip in this 20-min window for nests with more than one nestling (Stracey 2010). We conducted live observations with binoculars in 2009 in the parking lot. For the remainder of the sites we used video footage to conduct observations for 2008–2009. For each observation, we recorded number of nestlings and time, in minutes past sunset, of the last feeding trip. We conducted one observation in each of the following age groups: 0–4, 5–8, and 9–12 days since hatching and used average minutes past sunset for each nest in all analyses. Because of predation and random camera failure, we did not conduct observations within each age window for every nest.

We quantified light levels in all sites except the pasture (because of restricted access) at least 1 hr after dark. We did not control for lunar phase because differences in light levels across sites were far greater than what a full moon contributed (0.24 lux). An Extech EasyView light meter (Model EA31, range: 20–20,000 lux, resolution: 0.01 lux) was used to measure light levels. Because not all nests belonged to pairs for which we had territory maps, we restricted light level readings to a 20-m radius around the nest that included a variety of light microhabitats. For each nest, light level at the ground was measured every 5 m up to 20 m from the nest in three random directions. For each nest we averaged the 12 light recordings to obtain an average light level for the area around the nest. We excluded nests for which we could not obtain light meter readings from the regression analysis (see below). We tested for a correlation between number of nestlings and time of last feeding trip within each site. Because there was a significant correlation between number of nestlings and time of last feeding trip in the parking lot (Table 1), we included nestling number as a covariate in all subsequent analyses. We used linear regression to compare average light level (log transformed) near a nest to the time of the last feeding trip. We also tested for a difference across study sites in feeding time past sunset (square-root transformed) and average light level, and conducted pairwise comparisons between sites with a Tukey adjustment for multiple comparisons. All analyses were performed in SAS 9.2 (SAS Institute 2011).

TABLE 1. Correlation within each study site between nestling number and time of last feeding trip.

Site	r	n	P
Parking lot	0.32	17	0.019
Residential 1	0.07	13	0.37
Residential 2	0.001	12	0.94
Pasture	0.08	17	0.99
Preserve	0.16	21	0.072

RESULTS

We conducted nestling feeding observations on 80 nests. As light level (log transformed) increased, there was a significant increase in feeding time past sunset ($t_{1,42} = 3.61$, $P < 0.001$; Fig. 1). The effect of number of nestlings, which was included because of its correlation with time, was not significant in this model ($t_{1,42} = 1.20$, $P = 0.24$).

Site had a significant effect on the square-root of feeding time past sunset ($F_{4,74} = 8.03$, $P < 0.001$) with mockingbirds in the parking lot feeding their nestlings significantly later past sunset by ~15 mins than birds in other sites (Fig. 2). The effect of number of nestlings on feeding time past sunset was not significant ($F_{1,74} = 1.85$, $P = 0.18$). Average light level (log-transformed) varied by site ($F_{3,41} = 42.79$, $P < 0.001$) with all sites having different levels of light except for the two residential neighborhoods, which did not differ (Fig. 2).

DISCUSSION

As light levels increased, Northern Mockingbirds fed their nestlings later into the night

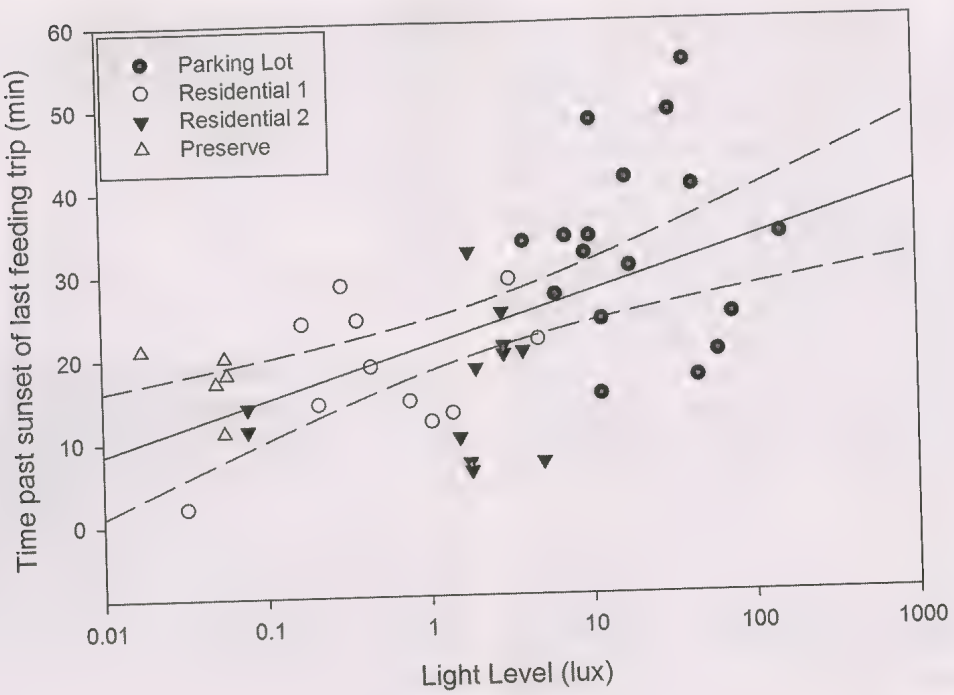


FIG. 1. Linear regression and 95% confidence interval (dashed lines) for all study sites combined, excluding the pasture, of minutes past sunset of last nestling feeding trip against log of light level ($y = 6.29x + 21.15$, $r^2 = 0.30$, $P < 0.001$). Symbols for study sites are for illustrative purposes only.

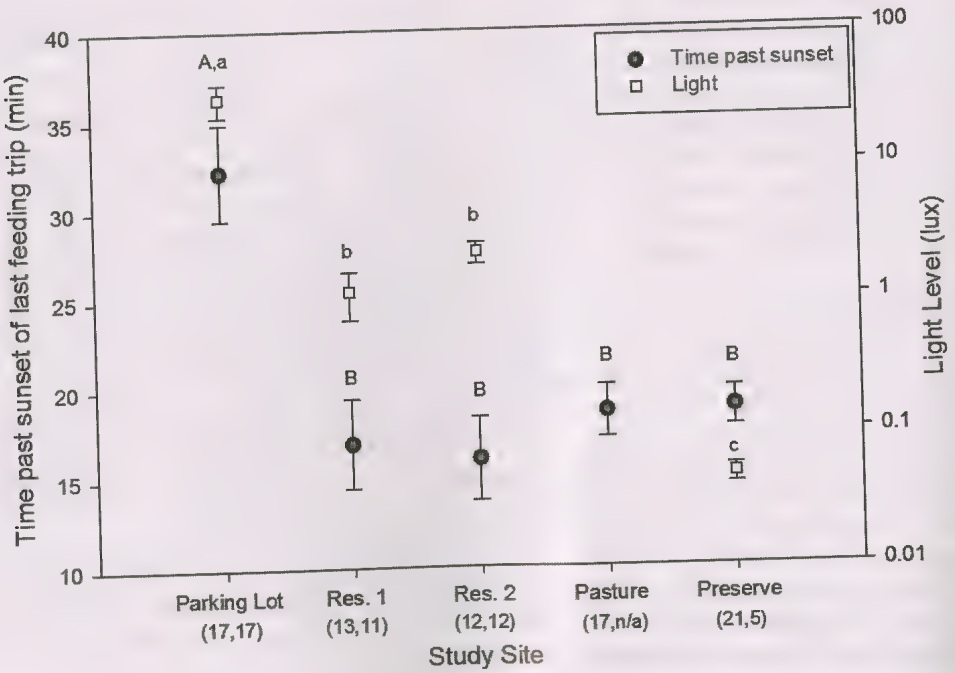


FIG. 2. Average (+/− SE) minutes past sunset of last nestling feeding trip and average light level (+/− SE; lux) at night within a 20-m radius of nests at six study sites. Res = residential site. Uppercase letters represent significance at experiment-wise $\alpha = 0.05$ for time past sunset comparisons; lowercase letters represent significance for light level comparisons. Numbers in parentheses represent sample sizes for time past sunset and light level, respectively.

(Fig. 1). Mockingbirds in the parking lot, which had the highest levels of light, fed their nestlings the latest past sunset (Fig. 2). These results support our hypothesis that light pollution creates conditions bright enough to allow diurnal species such as the mockingbird to feed their nestlings later into the night relative to birds in darker environments. Contrary to our prediction, however, birds at the residential sites, which contained street lights and light from houses, did not feed their nestlings later than birds in sites with no artificial lights (Fig. 1). These results suggest that there may be a threshold level of light necessary to elicit a behavioral response in foraging. To exploit the night light niche, mockingbirds may require sufficient light to allow them to effectively see prey or sufficient light to attract large numbers of insects.

Alternatively, night feeding may be determined by nestling condition and the parking lot may have been the only site where it was necessary for mockingbirds to feed at night. Stracey (2010) found that while prey delivered to mockingbird nestlings in urban habitats was smaller than prey delivered to non-urban nestlings, there were no differences in the number of feeding trips per nestling per hour or nestling mass amongst habitats. Mockingbirds in the parking lot may be compensating for reduced food quality by taking advantage of additional light to extend the number of feeding trips per day to the nest. The additional 15 mins of feeding time equates to approximately one extra trip per nestling (Stracey 2010); we do not know the biological significance of this. Studies in which artificial light levels are experimentally manipulated and food quality is simultaneously assessed will be necessary to determine why only parking lot mockingbirds fed their nestlings significantly later.

The ability of mockingbirds to behaviorally respond to artificial light might contribute to their success in urban habitats (Stracey 2010). The indirect effects of this altered behavior remain unknown. There may be costs associated with feeding later, such as increased stress on parent birds. Likewise, light pollution may alter patterns of mockingbird singing (Derrickson 1988), which in other species can have indirect fitness effects (Kempenaers et al. 2010). The potential indirect negative effects may be outweighed by potential positive direct effects, such as increased nestling growth and condition for mockingbirds. Future studies should identify the consequences of behavioral changes because of light pollution.

ACKNOWLEDGMENTS

We thank S. Daniels, T. J. Richard, and R. E. Hanauer for assistance with data collection and D. J. Levey for feedback on earlier versions of the manuscript. We thank the landowners, businesses, Ordway-Swisher Biological Station, and University of Florida Beef Research Unit for permission to work on their property. Funding provided by UF-HHMI G.A.T.O.R. Research Grant to BW, NSF Doctoral Dissertation Improvement Grant (grant # 0709646) to CMS, and Katharine Ordway Endowment of the Florida Museum of Natural History.

LITERATURE CITED

Derrickson, K. C. 1988. Variation in repertoire presentation in Northern Mockingbirds. Condor 90:592–606.

Derrickson, K. C. and R. Breitwisch. 1992. Northern Mockingbird (*Mimus polyglottos*). The birds of North America. Number 007.

Frank, K. D. 1988. Impact of outdoor lighting on moths: an assessment. Journal of the Lepidopterists' Society 42:63–93.

Garber, S. D. 1978. Opportunistic feeding behavior of *Anolis cristatellus* (Iguanidae: Reptilia) in Puerto Rico. Transactions of the Kansas Academy of Science 81:79–80.

Gaston, K. J., J. Bennie, T. W. Davies, and J. Hopkins. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biological Reviews 88:912–927.

Kempenaers, B., P. Borgström, P. Loës, E. Schlicht, and M. Valcu. 2010. Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. Current Biology 20:1735–1739.

Lebbin, D. J., M. G. Harvey, T. C. Lenz, M. J. Anderson, and J. E. Ellis. 2007. Nocturnal migrants foraging at night by artificial light. Wilson Journal of Ornithology 119:506–508.

Le Gros, A., C. M. Stracey, and S. K. Robinson. 2011. Associations between Northern Mockingbirds and the parasite *Philornis porteri* in relation to urbanization. Wilson Journal of Ornithology 123:788–796.

Longcore, T and C. Rich. 2004. Ecological light pollution. Frontiers in Ecology and the Environment 2:191–198.

SAS Institute. 2011. The SAS system for Windows. Release 9.2. SAS Institute, Inc., Cary, NC, USA.

Stracey, C. M. 2010. Patterns and processes in urban bird communities. Dissertation. University of Florida, Gainesville, Florida, USA.

Stracey, C. M. 2011. Resolving the urban nest predator paradox: The role of alternative foods for nest predators. Biological Conservation 144:1543–1550.

The Wilson Journal of Ornithology 126(2):370–373, 2014

Provisioning Behavior of Male and Female Indigo Buntings

Gary Ritchison[1,2] and Kimberly P. Little[1]

ABSTRACT.—The provisioning behavior of male and female songbirds varies among species, but most species exhibit biparental care. Our objective was to examine the provisioning behavior of male and female Indigo Buntings (*Passerina cyanea*), a species where males are reported to provide little or no parental care. Nests ($n = 16$) were video-taped during the 9-day nestling period and provisioning rates of adult buntings subsequently quantified. Provisioning rates of female buntings varied with nestling age, with 7–9-day old nestlings fed at higher rates than 1–6-day old nestlings. This increase was likely because of the increasing energy demands of nestlings. Male buntings provisioned nestlings at only three of 16 nests (18.8%), and primarily on days 7–9 post-hatching. Given the apparent relationships among paternal care, mating systems, and habitat characteristics, high-quality habitat may be an important factor contributing to reduced levels of paternal care by male buntings, along with opportunistic polygyny. Highly productive habitats with plentiful food resources may allow one parent to successfully care for young. Although habitats occupied by Indigo Buntings are apparently of sufficient quality to have favored a reduction in male parental care, variation in territory quality may require the contributions of some males to enhance nestling survival. *Received 13 September 2013. Accepted 20 December 2013.*

Key words: female-only care, habitat quality, *Passerina cyanea*, prey size, video-taping.

Among birds, provisioning nestlings is an important component of parental care, with the contributions of males and females varying among species. Among socially monogamous species, one sex may provision young most or all of the time; more often, however, both sexes provision but to varying degrees (Cockburn 2006). Most Indigo Buntings (*Passerina cyanea*) are socially monogamous, but previous studies have revealed high rates of extra-pair fertilizations (Westneat 1987, Hawks 1999). Male buntings are reported to provide little or no parental care (Carey and Nolan 1979; Westneat 1988a, b; Payne 1989), but the extent to which males provision nestlings and how provisioning behavior might vary among males or with nestling age have not been quantified. Similarly, the possible effect of males provisioning, or their lack of provisioning, on female provisioning rates has not been examined. Thus, our objective was to examine the provisioning behavior of male and female Indigo Buntings.

METHODS

We studied Indigo Buntings from May–August 1997 at the Miller Welch-Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. Beginning in early May, buntings were captured in mist nets and banded with a unique combination of a numbered USGS aluminum band and three colored-plastic bands. We located nests by monitoring the movements of females and searching potential suitable nest sites.

Nests that contained eggs were checked every 2 days to determine approximate hatch dates. Once a nest was located, we placed dummy cameras ~1–1.5 m from nests for 1 day prior to actual taping to allow habituation. Nests were taped using VHS camcorders at various times throughout the day (0700–1600 Eastern Daylight Time [EDT]), but with most taping from 0700–1200.

For each tape, we noted tape duration, nestling age (days 1–9 post-hatching), and number of nestlings present. For each nest visit, we noted whether it was the male or female and, if possible, the number of prey items delivered to nestlings. We also categorized prey size relative to bunting bill length (e.g., as long as a bunting's bill = prey size 1, twice as long as a bunting's bill = prey size 2, and so on). For each day, a measure of prey biomass delivered to nests was estimated by multiplying the total number of nest visits by mean prey size. Because of small sample sizes, we combined nestling ages (e.g., 1–2 days old) to examine possible age-related variation in nestling diet. Visit rate and biomass (visit rate multiplied by prey size) values were adjusted for brood size (i.e., per nestling).

[1] Department of Biological Sciences, Eastern Kentucky University, 521 Lancaster Avenue, Richmond, KY 40475, USA.

[2] Corresponding author; e-mail: gary.ritchison@eku.edu

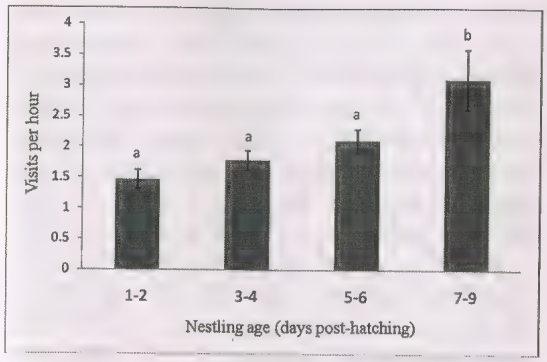


FIG. 1. Variation in mean provisioning rates (± SE) of female Indigo Buntings with increasing age of nestlings. Letters over bars show multiple comparisons from the Tukey's post-hoc test ($P < 0.05$), with different letters indicating significant differences.

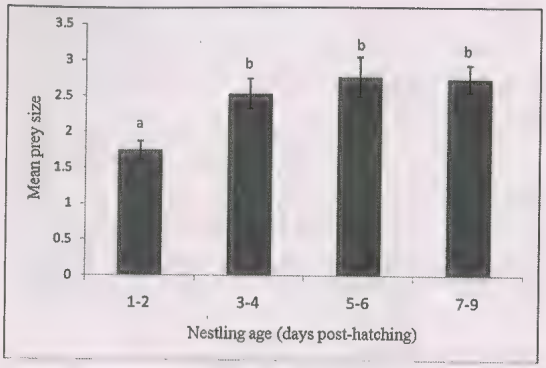


FIG. 2. Mean size of prey delivered (± SE) to nestlings of different ages by female Indigo Buntings ($n = 16$). Prey size was estimated relative to the length of the bunting bill. Inset letters over bars show multiple comparisons from the Tukey's post-hoc test ($P < 0.05$), with different letters indicating significant differences.

Because the same nests were videotaped on multiple days, we used repeated measures analysis of variance (ANOVA) to examine the effects of nestling age on provisioning rates by females, variation in prey size, and total biomass delivered. Tukey's post-hoc tests were used to compare means when differences were significant. Repeated measures ANOVA was also used to examine possible sex differences in size of prey delivered. Values are presented as means ± SE. All statistical analyses were conducted using Statistical Analysis System software (SAS Institute 2004).

RESULTS

Indigo Bunting nests ($n = 16$) were video-taped for 134 hrs (mean = 8.4 ± 2.1 hrs per nest). Mean brood size was 2.9 ± 0.6, with two broods with two nestlings, 13 with three, and one with four. Females primarily provisioned nestlings, but three males provisioned older nestlings.

Provisioning rates of females varied with nestling age ($F_{3,15} = 8.0$, $P < 0.001$), with 7–9-day old nestlings fed at higher rates than 1–6-day old nestlings (Tukey's test, $P < 0.05$; Fig. 1). The size of prey delivered to nestlings ($F_{8,22} = 2.6$, $P = 0.038$; Fig. 2) and estimated total biomass delivered also increased with nestling age ($F_{3,15} = 8.8$, $P = 0.001$; Fig. 3). Females delivered significantly smaller prey items to 1–2-day old nestlings than to older nestlings (Tukey's test, $P < 0.05$; Fig. 2), and also delivered more total biomass to older nestlings (Fig. 3).

We observed male Indigo Buntings provision nestlings at three of 16 nests (18.8%). With the exception of one visit to a nest by a male on day 4 post-hatching, all male provisioning occurred on days 7–9 post-hatching. Provisioning rates of the male bunting that provisioned nestlings most ($n = 61$ visits) increased from day 7 to day 9 post-hatching. On day 7 at this nest, adults made eight visits over a 2-hr period, with the male making one visit/hr and the female making three visits/hr. Over a 4-hr period on day 8, adults made 55 visits, with males making 6.8 visits/hr and females 7 visits/hr. During the course of 3.5 hrs on day 9, adults made 55 visits, with males making 9.1 visits/hr and females 6.6 visits/hr.

At a second nest that we recorded for 3.7 hrs on day 7 and again on day 9 post-hatching, the male made seven visits (18.4%) compared to 31 visits by the female on day 7, and he was not observed

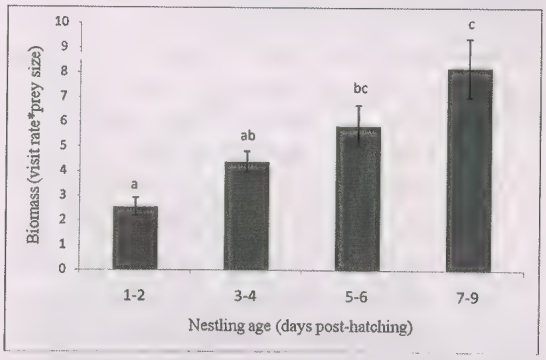


FIG. 3. Mean amount of estimated biomass (visit rate multiplied by prey size) delivered to nestlings of different ages (± SE) by female Indigo Buntings ($n = 16$). Inset letters over bars show multiple comparisons from the Tukey's post-hoc test ($P < 0.05$), with different letters indicating significant differences.

on day 9. A third nest was only videotaped for 2 hrs on one day (day 4 post-hatching), and the male and female each made one provisioning visit during that time.

For days 7–9 post-hatching when two males provisioned young, the mean size of prey delivered to nestlings by males (1.7 ± 0.1) and females (2.5 ± 0.1) did not differ ($F_{1,1} = 5.6$, $P = 0.25$). Similarly, provisioning rates of females (2.4 ± 0.2) and males (1.7 ± 0.4) did not differ ($F_{1,1} = 2.3$, $P = 0.37$).

DISCUSSION

Female Provisioning Behavior.—Female Indigo Buntings in our study provisioned 7–9-day old nestlings at higher rates than 1–6-day old nestlings. Similar results have been reported previously for Indigo Buntings (Morgan 1976, Dearborn et al. 1998) and other species of songbirds (Haggerty 1992, Nordlund and Barber 2005, Sethi and Bhatt 2007). Growth rates of nestlings in species with relatively short nestling periods, such as buntings, may remain relatively high throughout the nestling period (Ricklefs et al. 1998, Remeŝ and Martin 2002), and adults may respond by continuing to increase provisioning rates. However, in other species, provisioning rates during the nestling period exhibit a sigmoidal pattern, with rates increasing during the mid-nestling period and leveling off or even decreasing in the days prior to fledging (e.g., Moreno 1987, Barba et al. 2009). For species with longer nestling periods, growth rates and metabolic needs of young may level off or decline near the end of the nestling period (Murphy 1981, Ricklefs et al. 1998), and adult provisioning rates may do the same.

Female-Only Care.—Our results, and those of other investigators (Westneat 1988a, b; Payne 1989), indicate that female Indigo Buntings are primarily responsible for provisioning nestlings, with their mates providing little or no assistance. In a review of avian parental care, Cockburn (2006) noted that only 772 species of birds (or 8% of known species) exhibited female-only care. Most species that exhibit female-only care either have precocial young, or among altricial species, breed in the tropics and feed young fruit or nectar, foods that may be so abundant that male assistance in feeding young is not necessary (Cockburn 2006). Few species with female-only care are insectivorous, and most that are breed in tropical rainforests (Cockburn 2006). Thus, Indigo Buntings are among the few species of birds with female-only or nearly female-only care that are insectivorous and breed at temperate latitudes.

Three of 16 male Indigo Buntings (18.8%) provisioned nestlings in our study, primarily during the three days prior to fledging. Similarly, male buntings fed nestlings at 10% of nests observed in Michigan and Indiana (Carey and Nolan 1979, Payne 1989), and at 12% of nests in Missouri (Dearborn et al. 1998). Among birds, paternal care of nestlings varies with mating system, and mating systems, in turn, may vary with habitat quality. For example, Leisler et al. (2002) conducted a phylogenetic analysis of parental care and mating system characteristics relative to ecological traits for 17 species of Acrocephaline warblers and concluded that male parental care decreased as habitat quality and productivity increased. Levels of paternal care also tend to coevolve with mating systems, with reduced paternal care typical of species with polygynous or promiscuous mating systems (Leisler et al. 2002). Although generally considered socially monogamous (Payne 2006), about 10 to 15% of male Indigo Buntings are polygynous in some populations (Carey and Nolan 1979, Payne 2006) and extrapair fertilizations are common, e.g., 35% of young in a population in North Carolina (Westneat 1990) and 44% in a population in Kentucky (Hawks 1999). Given the apparent relationships between mating systems, paternal care, and habitat quality (Leisler et al. 2002), habitat quality is likely an important factor contributing to male Indigo Buntings' tendencies to limit their parental care, engage in occasional polygyny, and have relatively high rates of promiscuous mating.

Male Provisioning.—Only three of 16 male Indigo Buntings provisioned nestlings in our study, but studies of other facultatively polygynous species with reduced paternal care, including European Starlings (*Sturnus vulgaris*; Pinxten and Eens 1994), Red-winged Blackbirds (*Agelaius phoeniceus*; Muldal et al. 1986), Dickcissels (*Spiza americana*; Igl and Best 2001), and House Wrens (*Troglodytes aedon*; Johnson et al. 1993), have revealed that provisioning by males can improve fledging success. This may be particularly true when environmental conditions (e.g., drought) cause a reduction in food availability (Wittenberger 1982, Igl and Best 2001). The possible effect of male provisioning on fledging success in Indigo Buntings has not been exam-

ined. However, studies have demonstrated that the provisioning of fledglings by male Indigo Buntings allows their mates to initiate re-nesting sooner than if unaided (Westneat 1987, 1988b; Payne 1989). Thus, if provisioning of nestlings by male buntings allows females to reduce their efforts and begin preparing to re-nest, or if male buntings that provision nestlings also provision fledglings, one potential benefit for those relatively few males that assist in provisioning older nestlings may be that mates re-nest sooner, potentially increasing male reproductive success.

ACKNOWLEDGMENTS

We thank Donna Hardin for assisting with field work, Steve Campbell for statistical advice, and Mary Brown and two anonymous reviewers for comments that improved our manuscript.

LITERATURE CITED

BARBA, E., F. ATIÉNZAR, M. MARÍN, J. S. MONRÓS, AND J. S. GIL-DELGADO. 2009. Patterns of nestling provisioning by a single-prey loader bird, Great Tit *Parus major*. Bird Study 56:187–197.

CAREY, M. AND V. NOLAN JR. 1979. Population dynamics of Indigo Buntings and the evolution of avian polygyny. Evolution 33:1180–1192.

COCKBURN, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B 273:1375–1383.

DEARBORN, D. C., A. D. ANDERS, F. R. THOMPSON III, AND J. FAABORG. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100:326–334.

HAGGERTY, T. M. 1992. Effects of nestling age and brood size on nestling care in Bachman's Sparrow (*Aimophila aestivalis*). American Midland Naturalist 128: 115–125.

HAWKS, J. M. 1999. Effect of mate quality on the mating strategies of female Indigo Buntings: a genetic analysis. Thesis. Eastern Kentucky University, Richmond, USA.

IGL, L. D. AND L. B. BEST. 2001. On the rarity of observations of food provisioning by male Dickcissels. Prairie Naturalist 33:111–118.

JOHNSON, L. S., L. H. KERMOTT, AND M. R. LEIN. 1993. The cost of polygyny in the House Wren *Troglodytes aedon*. Journal of Animal Ecology 62:669–682.

LEISLER, B., H. WINKLER, AND M. WINK. 2002. Evolution of breeding systems in Acrocephaline warblers. Auk 119:379–390.

MORENO, J. 1987. Parental care in the Wheatear *Oenanthe oenanthe* - effects of nestling age and brood size. Ornis Scandinavica 18:291–301.

MORGAN, F. D. 1976. Nesting studies of the Indigo Bunting (*Passerina cyanea*) at Thornhill, Indiana. Indiana Academy of Science 86:461–465.

MULDAL, A. M., J. D. MOFFATT, AND R. J. ROBERTSON. 1986. Parental care of nestlings by male Red-winged Blackbirds. Behavioral Ecology and Sociobiology 19:105–114.

MURPHY, M. T. 1981. Growth and aging of nestling Eastern Kingbirds and Eastern Phoebes. Journal of Field Ornithology 52:309–316.

NORDLUND, C. A. AND C. A. BARBER. 2005. Parental provisioning in *Melospiza melodia* (Song Sparrows). Northeastern Naturalist 12:425–432.

PAYNE, R. B. 1989. Indigo Bunting. Pages 153–172 *in* Lifetime reproduction in birds (I. Newton, Editor). Academic Press, London, UK.

PAYNE, R. B. 2006. Indigo Bunting (*Passerina cyanea*). The birds of North America. Number 4.

PINXTEN, R. AND M. EENS. 1994. Male feeding of nestlings in the facultatively polygynous European Starling: allocation patterns and effect on female reproductive success. Behaviour 129:113–140.

REMEŠ, V. AND T. E. MARTIN. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518.

RICKLEFS, R. E., J. M. STARCK, AND M. KONARZEWSKI. 1998. Internal constraints on growth in birds. Pages 266–287 *in* Avian growth and development (J. M. Starck and R. E. Ricklefs, Editors). Oxford University Press, Oxford, UK.

SAS INSTITUTE. 2004. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

SETHI, V. K. AND D. BHATT. 2007. Provisioning of young by the Oriental Magpie-Robin (*Copsychus saularis*). Wilson Journal of Ornithology 199:356–360.

WESTNEAT, D. F. 1987. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. Animal Behaviour 35:877–886.

WESTNEAT, D. F. 1988a. Male parental care and extrapair copulations in the Indigo Bunting. Auk 105:149–160.

WESTNEAT, D. F. 1988b. The relationships among polygyny, male parental care, and female breeding success in the Indigo Bunting. Auk 105:372–374.

WESTNEAT, D. F. 1990. Genetic parentage in the Indigo Bunting: a study using DNA fingerprinting. Behavioral Ecology and Sociobiology 27:67–76.

WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84:22–39.

The Wilson Journal of Ornithology 126(2):374–381, 2014

Factors Influencing Seed Species Selection by Wild Birds at Feeders

Stacey M. Johansen,[1] David J. Horn,[1,2] and Travis E. Wilcoxen[1]

ABSTRACT.—Seed preferences of wild birds may be a result of factors such as bill and seed morphology, handling time, nutritional content of the seed, and foraging behavior of the bird. To examine factors influencing seed choice of 10 species of birds that regularly visit bird feeders in the United States and Canada, we collected data on bird visits, bill size, seed size, and nutritional content of seeds for 10 seed types commonly used in bird seed blends. The presence of an outer hull, protein content, and the ratio of bill volume to seed volume were the most important variables determining seed choice. Fiber and fat content were less important. Results from this study help us understand why birds that use feeders use the seed types they do, and ultimately, may improve the composition of seed species and individual seeds found in bird food blends.
Received 1 May 2013. Accepted 12 February 2014.

Key words: bird feeding, bird food, citizen science, food preferences, seed characteristics, supplemental feeding.

In 2011, more than $5 billion was spent on bird food, feeders, and other products by over 52 million Americans (U.S. Fish and Wildlife Service 2012). Bird food recommendations are found in books, magazines, newspaper articles, and websites (e.g., Harrison and Harrison 1983, Burton 1995, Dunn and Tessaglia-Hymes 1999), and have been studied scientifically (Geis 1980, Horn 1999, Horn et al. 2014). However, fewer studies have examined why birds prefer certain seed species over others. Research questions that require large geographic areas and/or long timescales, such as studies on wild bird feeding, may be best addressed using citizen science (Bonney et al. 2009, Silvertown 2009, Dickinson et al. 2010). Citizen science is the collection of data by public volunteers, which can be used by scientists to answer research questions (Thumbull et al. 2000, Bonter and Hochachka 2009, Dickinson et al. 2010). The use of citizen scientists in research has been implemented worldwide within fields ranging from evolutionary biology to global climate change, and is regularly used in ornithology studies (Silvertown 2009, Dickinson et al. 2010).

Previous studies of seed preferences have examined the role of nutritional and anti-nutritional content, seed size, bill size, handling time, and behavior of the bird (Pyke et al. 1977, Díaz 1990, Díaz 1996, Hayslette and Mirarchi 2001, Hrabar and Perrin 2002, van der Meij et al. 2004, Hayslette 2006, Collins and Horn 2012, Ríos et al. 2012a, b). For example, the seed preferences of Northern Cardinals (*Cardinalis cardinalis*) and Song Sparrows (*Melospiza melodia*) were more associated with seed handling time than other characteristics (Willson and Harmeson 1973), and seed handling time can be affected by physical characteristics of the seed (Hrabar and Perrin 2002). One way to assess energy content within a seed type is mass of the seed (but see Pulliam 1980). Heinrich et al. (1997) found that Black-capped Chickadees (*Poecile atricapillus*) and Red-breasted Nuthatches (*Sitta canadensis*) preferred heavier sunflower seeds over lighter ones. Assuming that differences in handling time between two seeds of the same species are not significant, heavier seeds may provide greater energy content.

We studied how characteristics of the seed type including fat, fiber, and protein content, presence of an outer seed hull, and the ratio of bill to seed volume influenced the number of bird visits to common seed species found in bird food blends through a field study. By understanding factors that influence seed use in a setting where birds have the choice to visit supplemental foods, producers can develop hybrid seeds, and wild bird food companies may produce seed blends that are most attractive to birds based on seed physical and nutritional characteristics. We hypothesized that fat content and the ratio of bill to seed volume would be the most important factors in seed selection as Collins and Horn (2012) found oil content and seed shape to influence seed consumption and number of bird visits of common species that use supplemental food.

[1] Department of Biology, Millikin University, 1184 West Main Street, Decatur, IL 62522, USA.
[2] Corresponding author; e-mail: dhorn@millikin.edu

METHODS

Bird Seed Use.—A complete description of the methods used to collect seed use data is found in Horn et al. (2014). The study began in winter 2005 and continued through fall 2008, and we used 173 volunteers to collect data. We used locations throughout the U.S. and Canada (excluding Alaska and Hawaii) representing six geographic regions defined by the Partners in Flight North American Landbird Conservation Plan: Eastern (n = 57 observers), Intermountain West (n = 20), Northern Forest (n = 18), Pacific (n = 6), Prairie (n = 68), and Southwest (n = 4) (Rich et al. 2004).

Participants were provided four feeders of the same model, four shepherd's hooks or poles for hanging or mounting feeders, four squirrel or raccoon baffles, and 10 types of bird seed: black-oil sunflower (*Helianthus annuus*), cracked corn (*Zea mays*), fine sunflower chips (black-oil sunflower with its outer hull removed), medium sunflower chips, Nyjer® (*Guizotia abyssinica*, also known as thistle), red milo (*Sorghum bicolor*, also known as sorghum), safflower (*Carthamus tinctorius*), striped sunflower (*H. annuus*), white proso millet (*Panicum miliaceum*), and whole peanuts (*Arachis hypogaea*, peanuts out of the shell and split in half). Fine sunflower chips were defined as being seeds that could fit through a 0.3-cm round-hole screen and over a 0.2-cm screen, while medium sunflower chips could fit through a 0.5-cm round-hole screen and over a 0.3-cm screen. The 10 seed species used were selected as they are among the most common types sold as bird seed. The four feeders of the same model were one of three general types: hopper, platform, and tube. We used the following tube feeder models: Artline 6145 (Hillside, IL), and Droll Yankees A-6F, CJM-15G, and CJM-23G (Plainfield, CT). The hopper feeder models we used included Heath Outdoor Products 152 and 184 (Coopersville, MI), Heritage Farms 7511i (Antioch, IL), a Perky Pet feeder (Lititz, PA), and Wild Bird Centers of America, Inc.'s Mobi Hopper Feeder 2-sided Medium (Glen Echo, MD). Platform feeders included uncovered wood and recycled plastic feeders (31 × 38 cm with 5 cm sides) by Backyard Nature Products (Chilton, WI), Cabin Fever Fly-through Feeder (Bozeman, MT), Droll Yankees GS1, and Wild Bird Centers of America, Inc.'s Covered Platform Feeder. When the supplies arrived, volunteers placed the four bird feeders in a straight line 2 m apart from one another with each feeder containing a single type of bird seed.

Participants committed to the study for four consecutive seasons for 1 year. The seasons were spring (Mar 20–Jun 20), summer (Jun 21–Sep 21), fall (Sep 22–Dec 20), and winter (Dec 21–Mar 19). During each season, monitoring took place every other day for 64 days. The 10 seed types used during the 64-day period were presented and rotated in a systematic manner, and each citizen scientist was assigned a unique rotation schedule with the seed combination and initial position of the seed assigned randomly. During each of the 32 monitoring sessions that took place each season, the number of birds of each species at each feeder was recorded every 5 min over a 45-min period.

Seed Use Values.—We calculated seed use values for each combination of bird species and seed species using linear mixed models and PASW 18.0 software (SPSS, Inc. 2009). For species that are in the same geographic region year-round, we used a mixed model analysis with the fixed effects: seed type (10 levels), feeder type (3 levels), season (4 levels), geographic region (6 levels), seed type × feeder type interaction (30 levels), and seed type × season interaction (40 levels). For species that move among geographic regions during the year (e.g., American Goldfinch [*Spinus tristis*] and Common Grackle [*Quiscalus quiscula*]), we ran the mixed model above without the seed type × season interaction. For all of the mixed models, we used the random variable "observer" (173 levels) to account for the repeated measures made by citizen scientists at a site, differences among citizen scientists among sites, and differences in bird communities and microhabitats among sites. To account for yearly differences in the abundance of birds, a second covariance parameter in all of the mixed models we ran was year. For the mixed models, the mean number of birds of each species derived from the 10 counts at each feeder within a 45-min session, and the resulting marginal means, were used as a measure of relative seed use by 10 bird species (Table 1).

Seed Size and Nutritional Content.—Nutritional content (% fat, fiber, and protein) of each seed type was determined at Eurofins Scientific Inc., Des Moines, IA, USA (Table 2; % fat determined through ether extraction technique and % protein determined through combustion technique). Seed

TABLE 1. Seed use by 10 bird species in the United States and Canada, winter 2005–fall 2008, during 20,077, 45-min observation sessions at feeders (number of bird visits recorded ranged from 6,625 for Downy Woodpeckers to 305,087 for House Sparrows). Marginal mean number of birds of each species per 5-min recording within a 45-min monitoring session are displayed.

	Seed type[a]									
Species	BOS	CC	FSC	MSC	N	RM	S	SS	WPM	WP
American Goldfinch	0.64	0.23	0.71	0.73	0.85	0.23	0.26	0.32	0.26	0.22
Black-capped Chickadee	0.21	0.00	0.07	0.12	0.00	0.00	0.06	0.06	0.00	0.04
Common Grackle	0.05	0.07	0.05	0.05	0.01	0.03	0.02	0.05	0.03	0.05
Downy Woodpecker	0.01	0.00	0.02	0.02	0.00	0.00	0.00	0.01	0.00	0.01
House Finch	0.71	0.23	0.56	0.58	0.52	0.25	0.47	0.41	0.23	0.34
House Sparrow	0.05	0.05	0.03	0.02	0.00	0.00	0.00	0.00	0.70	0.00
Mourning Dove	0.02	0.01	0.02	0.01	0.02	0.01	0.03	0.00	0.07	0.00
Northern Cardinal	0.11	0.00	0.01	0.03	0.00	0.00	0.04	0.06	0.00	0.00
Tufted Titmouse	0.04	0.00	0.02	0.03	0.00	0.00	0.02	0.03	0.05	0.00
White-breasted Nuthatch	0.03	0.00	0.02	0.02	0.00	0.00	0.00	0.02	0.00	0.03

[a] Seed types include black-oil sunflower (BOS), cracked corn (CC), fine sunflower chips (FSC), medium sunflower chips (MSC), Nyjer (N), red milo (RM), safflower (S), striped sunflower (SS), white proso millet (WPM), and whole peanuts (WP).

size was determined by taking measurements of the length, width, and depth of 40 seeds of each species using a Mitutoyo Absolute Digimatic Caliper CD-6 CSX (Table 3). Each measurement was taken twice and averaged. To reduce the variation within a seed species, all seeds met Wild Bird Feeding Industry Quality Standards.

Bill Measurements.—We took measurements of the culmen length, bill width, and bill depth of 363 individual birds of 10 species within the museum collections at the Illinois State Museum, Springfield, IL, USA and Illinois State University, Bloomington, IL, USA. We measured an individual bill twice then averaged the two values. We took measurements of: American Goldfinches (n = 50 specimens measured), Black-capped Chickadees (n = 26), Common Grackles (n = 57), Downy Woodpeckers (*Picoides pubescens*, n = 35), House Finches (*Haemorhous mexicanus*, n = 25), House Sparrows (*Passer domesticus*, n = 50), Mourning Doves (*Zenaida macroura*, n = 21), Northern Cardinals (n = 50), Tufted Titmice (*Baeolophus bicolor*, n = 23), and White-breasted Nuthatches (*Sitta carolinensis*, n = 26).

Statistical Analysis.—We used linear mixed models (LMM) to determine how seed use was influenced by seed size, seed nutritional content, and the ratio of bill to seed volume. Specifically, independent variables used to construct models included three measures of nutritional content of the seed (% fat, fiber, protein), whether or not the seed had an outer hull, the average volume of the seed type, and the ratio of bill volume to seed volume (ratio). The dependent variable, frequency of seed use by that species, was determined from estimated marginal means from a mixed model as described above.

To determine the best model explaining factors influencing seed choice, we used an information-theoretical approach wherein we utilized a second-order Akaike's Information Criterion derived from LMM to evaluate a set of candidate models (AICc; Burnham and Anderson 2002) for each species. Models were ranked and evaluated

TABLE 2. Fat, fiber, and protein content (%) of 10 seed types commonly used in bird seed blends.

	Seed type[a]									
%	BOS	CC	FSC	MSC	N	RM	S	SS	WPM	WP
Fat	43	2	55	56	40	2	38	26	4	45
Fiber	13	2	3	4	14	2	21	20	6	2
Protein	16	8	24	24	22	11	14	23	11	24

[a] Seed types include black-oil sunflower (BOS), cracked corn (CC), fine sunflower chips (FSC), medium sunflower chips (MSC), Nyjer (N), red milo (RM), safflower (S), striped sunflower (SS), white proso millet (WPM), and whole peanuts (WP).

TABLE 3. Mean seed length, width, and depth (mm) of 10 seed types commonly used in bird seed blends.

Measure (mm)	Seed type[a]									
	BOS	CC	FSC	MSC	N	RM	S	SS	WPM	WP
Length	9.6	6.8	3.0	5.8	4.2	4.1	7.2	14.6	2.7	13.3
Width	4.9	4.1	1.9	3.4	1.2	3.7	3.8	6.7	2.2	6.7
Depth	2.3	2.8	1.2	1.9	1.0	2.5	2.8	3.2	1.7	7.9

[a] Seed types include black-oil sunflower (BOS), cracked corn (CC), fine sunflower chips (FSC), medium sunflower chips (MSC), Nyjer (N), red milo (RM), safflower (S), striped sunflower (SS), white proso millet (WPM), and whole peanuts (WP).

according to ΔAICc, which is the difference between the AICc values of a given model and that of the best model. Models with $\Delta AICc > 2.0$ are considerably less informative than the best model (Burnham and Anderson 2002). We calculated Akaike's Weights (w_i), which convert the deviance of all possible models to a scale of zero to one; each weight then represents the likeliness that the model is the best model. In addition to the model selection analysis, we calculated McFadden's pseudo-r^2 (Cameron and Windmeijer 1996) to estimate the explanatory power of the best model for each species and also determined relative variable importance for each variable in the analyses (Burnham and Anderson 2002).

We began the analysis with an LMM with the categorical independent variable, whether or not the seed has a hull, as a fixed factor, and the remaining, continuous, independent variables as covariates. We also included two-way interactions. This was used as the global model. Subsequent models were constructed using all possible combinations of variables for main effects and possible two-way interactions between factors and covariates. Only models with a pseudo-$r^2 > 0.2$ were interpreted, and independent variables with a relative variable importance >0.2 were considered significant factors influencing seed choice.

There are several factors inherent in a field study that we were not able to control such as changes in flock size at feeders, inter- and intraspecific competition at feeders, weather conditions, and microhabitat including the presence of perching and caching sites (e.g., Balph and Balph 1976). However, given the extremely large number of observations (>20,000 45-min observations) with thousands of counts at each food item across seasons, regions, years, and observers, as well as our statistical analysis that accounts for such variation, it is unlikely that these factors resulted in a systematic bias in our results.

RESULTS

Of the 10 species examined, seven had best models with a pseudo-$r^2 > 0.2$. The most important factors influencing seed choice included presence of an outer hull and protein content ($n = 6$ of 7 species each), and ratio of bill to seed volume ($n = 5$ species, Table 4). Fat ($n = 3$) and fiber ($n = 1$) content influenced fewer species. The average volume of the seed type was not a significant variable in any of the best models for any species. For the six species for which a nutritional content variable was important, Black-capped Chickadee, Tufted Titmouse, Northern Cardinal, Common Grackle, House Finch, and American Goldfinch, greater levels of fat, fiber and/or protein resulted in greater selection of that seed species.

Mourning Doves selected seeds with hulls (relative variable strength = 0.86) and a greater bill to seed volume ratio (0.82). Black-capped Chickadees selected seeds with a lower bill to seed volume ratio (0.89), seeds without hulls (0.72), and greater protein (0.22) and fat (0.20) levels. Tufted Titmice selected seeds with a lower bill to seed volume ratio (0.94), and greater levels of protein (0.57) and fat (0.35). Northern Cardinals were most likely to visit sites with seed species that had hulls (0.93) and greater fiber (0.46) and protein (0.27) content. Seeds without hulls (0.99), smaller bill to seed volume ratio (0.75), and greater protein (0.20) were the most important factors for Common Grackles. House Finches' seed use was greater at seeds with hulls (0.93), and with greater fat (0.65) and protein content (0.22). American Goldfinches were more likely to select seed species with a greater bill to seed volume ratio (0.89), without hulls (0.66), and greater levels of protein (0.30). Factors that we examined were not good predictors of seed choice

TABLE 4. Model results examining relationships among bird use of 10 seed types with presence of an outer hull, ratio of bill volume to seed volume, and nutritional content of the seed, for 10 species of birds. The direction of the preference is included in parentheses after each variable name. For the categorical variable "hull," a (+) indicates that the preference was for seeds with hulls, and a (−) indicates that the preference was for seeds without hulls. For all other variables, a (+) indicates a preference for greater values within that variable, and a (−) indicates a preference for lower values within that variable. Only models with Akaike's weights >0.10 plus the global and null models are shown. Models were ranked to w_i.

Species + Model	−2LL[a]	AICc[b]	ΔAICc[c]	K[d]	w_i[e]
American Goldfinch (pseudo-r^2 for best model = 0.41)					
Hull (−) + Ratio (+)	5.28	8.08	0.00	4	0.517
Fat (+) + Ratio (+)	7.40	10.20	2.12	4	0.179
Protein (+) + Ratio (−)	7.94	10.74	2.66	4	0.137
Hull (−) + Protein (+)	8.52	11.32	3.24	4	0.102
Null	16.24	18.64	10.64	0	0.000
Global	34.32	40.32	32.24	8	0.000
Black-capped Chickadee (pseudo-r^2 for best model = 0.43)					
Hull (−) + Ratio (−)	−11.80	−9.04	0.00	4	0.600
Fat (+) + Ratio (−)	−9.15	−6.35	2.69	4	0.156
Null	18.28	20.86	29.90	0	0.000
Global	26.49	28.59	37.63	8	0.000
Common Grackle (pseudo-r^2 for best model = 0.30)					
Hull (−) + Ratio (−)	−32.12	−29.32	0.00	4	0.743
Hull (−) + Protein (+)	−29.44	−26.64	2.68	4	0.194
Global	23.58	29.58	58.90	8	0.000
Null	40.39	42.97	72.29	0	0.000
Dark-eyed Junco (pseudo-r^2 for best model = 0.28)					
Hull (+) + Ratio (+)	−35.42	−32.62	0.00	4	0.689
Ratio (+) + Protein (−)	−31.58	−28.78	3.84	4	0.101
Global	19.75	25.75	58.37	8	0.000
Null	46.88	49.54	82.16	0	0.000
Downy Woodpecker (pseudo-r^2 for best model = 0.20)					
Hull (−) + Protein (+)	− 48.14	−45.34	0.00	4	0.637
Hull (−) + Fat (+)	−45.79	−42.99	2.35	4	0.197
Null	−7.35	−9.95	35.39	0	0.000
Global	13.00	19.00	64.34	8	0.000
House Finch (pseudo-r^2 for best model = 0.39)					
Hull (+) + Fat (+)	0.60	3.40	0.00	4	0.570
Hull (+) + Protein (+)	3.36	6.16	2.76	4	0.143
Hull (+) + Fiber (+)	4.02	6.82	3.42	4	0.103
Null	5.84	7.91	4.51	0	0.080
Global	33.64	39.64	36.24	8	0.000
House Sparrow (pseudo-r^2 for best model = 0.01)					
Null	0.45	3.02	0.00	0	0.622
Hull (−) + Fiber (−)	7.34	10.14	7.12	4	0.108
Global	40.32	46.32	43.30	8	0.000
Mourning Dove (pseudo-r^2 for best model = 0.32)					
Hull (+) + Ratio (+)	−30.00	−27.20	0.00	4	0.685
Null	−3.98	−2.39	24.81	0	0.000
Global	21.90	27.90	55.10	8	0.000
Northern Cardinal (pseudo-r^2 for best model = 0.49)					
Hull (+) + Fiber (+)	−18.87	−16.07	0.00	4	0.413
Hull (+) + Protein (+)	−17.64	−14.84	1.23	4	0.223
Hull (+) + Ratio (−)	−16.84	−14.04	2.03	4	0.150
Hull (+) + Fat (+)	−16.75	−13.95	2.12	4	0.143

TABLE 4 Continued.

Species + Model	−2LL[a]	AICc[b]	ΔAICc[c]	K[d]	w_i[e]
Null	−3.24	−1.09	14.98	0	0.000
Global	29.15	35.15	51.22	8	0.000
Tufted Titmouse (pseudo-r^2 for best model = 0.23)					
Ratio (−) + Protein (+)	−34.13	−31.33	0.00	4	0.538
Ratio (−) + Fat (+)	−33.19	−30.39	0.94	4	0.336
Null	−4.41	−2.16	29.17	0	0.000
Global	15.77	21.77	53.10	8	0.000
White-breasted Nuthatch (pseudo-r^2 for best model = 0.19)					
Ratio (−) + Protein (+)	−41.55	−38.75	0.00	4	0.785
Null	−15.17	−12.24	26.31	0	0.000
Global	14.75	20.75	59.50	8	0.000

[a] −2 log likelihood defines the maximum likelihood estimate.
[b] Akaike's Information Criterion corrected for small sample size relative to number of parameters.
[c] Change in AICc score from the best model to the model of interest.
[d] Number of parameters in the model.
[e] Relative weight of the model, representing the likelihood that this is, in fact, the best model.

(pseudo- $r^2 \leq 0.2$) for Downy Woodpeckers, White-breasted Nuthatches, and House Sparrows.

DISCUSSION

Most of the previous research on seed choice has focused on only a small number of species, often only one species, in a single geographical location. Our study examined seed choice by many species across the United States and Canada and directly compares the importance of multiple factors to seed choice by birds. Characteristics of the seed (i.e., presence of an outer hull) and bird (i.e., bill volume to seed volume ratio) were two of the most important factors influencing seed species selection by wild birds that use feeders. These factors, along with the size and shape of seeds, could be associated with handling time and have been shown to be important in previous studies (Willson 1972, Hayslette 2006, Collins and Horn 2012). Willson (1972) found that Song Sparrows, American Tree Sparrows (*Spizella arborea*), and Dark-eyed Juncos (*Junco hyemalis*) preferred short, thin seeds, and Hayslette (2006) found Mourning Doves selected corn that was shorter and thinner than average. Horn et al. (2014) found that many species prefer black-oil sunflower to sunflower chips even though sunflower chips have lower handling time. Some species cache seeds (e.g., Black-capped Chickadees, Tufted Titmice, and White-breasted Nuthatches), and for these species, the husk may be an important characteristic that protects the seed embryo from decomposition at the cache site. However, none of the species that take a seed from a feeder and consume the seed elsewhere were positively affected by the presence of a hull in our study. Collins and Horn (2012) found that seed consumption by all species combined was greater at higher oil content, black-oil sunflower seed compared to lower oil content seed when seed size was equivalent. However, House Finches, American Goldfinches, and House Sparrows had equivalent visits to shorter, deeper, seeds with lower oil-content compared to larger, higher oil-content seeds, when both varieties were present indicating that both handling time and nutritional content of the seed are important factors in seed choice (Collins and Horn 2012).

The most important nutritional component influencing seed species selection in this study was protein content. Compared to invertebrates, seeds are a poor source of protein (Díaz 1996, Hayslette and Mirarchi 2001). Thus, granivorous birds should select seeds highest in protein to meet their requirements. Two of the three seed types with the least amount of protein, cracked corn and red milo, are seed types with fewer bird visits. On the contrary, white proso millet has a low amount of protein, but comparatively greater number of bird visits. Bird visits may be higher for white proso millet because its smaller size leads to larger bill volume to seed volume ratios for species such as the Mourning Dove; a species that is most abundant at white proso millet.

Three species selected seeds with higher levels of fat. The seed type with the greatest abundance of birds (black-oil sunflower for Black-capped Chickadees and House Finches, and black-oil

sunflower and whole peanuts for Tufted Titmice) contained a fat content >40%. The selection of higher fat seeds by Black-capped Chickadees and Tufted Titmice may be a result of their behavior in which they take a seed at a feeder and go elsewhere to eat. For these species, selecting high fat seeds that maximize energy gain may be better in offsetting the costs of flying to and from the feeder (Lima 1985). On the contrary, for species that perch and eat at a feeder, fat content may be less important. However, Browning et al. (1981) found that Northern Cardinals selected seed species with the greatest levels of both protein and fat, lowest levels of fiber, and greatest energy content. Certain seed species in bird food blends including black-oil sunflower, medium sunflower chips, and white proso millet are selected by wild birds over others (Geis 1980, Horn 1999, Horn et al. 2014), and seed species selection is dependent on factors such as handling time, nutritional content, and bird behavior (Díaz 1996, Hayslette and Mirarchi 2001, Hrabar and Perrin 2002, Hayslette 2006, Collins and Horn 2012). Knowing which seed types are most selected and factors influencing their selection can result in the development of better bird seed blends, and reduce potential negative consequences of bird feeding. Raccoons (*Procyon lotor*) and black bears (*Ursus americanus*) regularly frequent bird feeders (Barden et al. 1995, Hristienko and McDonald 2007), and to what extent these and other mammals are attracted to unused seed that falls to the ground warrants further study. Furthermore, some seed types, under certain conditions, can produce fungal metabolites, including aflatoxins (Henke et al. 2001). Thus, using seed ingredients that are most selected by birds, and introducing new hybrids or new ingredients into seed blends based on physical and nutritional characteristics, could lead to a better bird feeding experience for wild birds and the people who feed them.

ACKNOWLEDGMENTS

We gratefully acknowledge the dedicated wild bird feeding enthusiasts throughout the United States and Canada who participated in the study. Funding for this study was provided by the WBFI (Wild Bird Feeding Industry) and its member companies, grants from Kaytee Avian Foundation and National Sunflower Association, as well as individuals who financially supported the WBFI Research Foundation through cash and in-kind contributions. We thank L. A. Lundstrom for reviewing the manuscript prior to submission.

LITERATURE CITED

Balph, M. H. and D. F. Balph. 1976. Some factors influencing observed sex ratios in a population of Evening Grosbeaks. Bird-Banding 47:340–344.

Barden, M. E., D. Slate, R. T. Calvert, and P. W. Debow. 1995. Strategies to address human conflicts with raccoons and black bears in New Hampshire. Proceedings of the Eastern Wildlife Damage Control Conference 6:22–29.

Bonney, R., C. B. Cooper, J. Dickinson, S. Kelling, T. Phillips, K. V. Rosenberg, and J. Shirk. 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience 59:977–984.

Bonter, D. N. and W. M. Hochachka. 2009. A citizen science approach to ornithological research: twenty years of watching backyard birds. Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics 4:453–458.

Browning, N. G., A. D. Dayton, and R. J. Robel. 1981. Comparative preferences of Field Sparrows and cardinals among four propagated seeds. Journal of Wildlife Management 45:528–533.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference, a practical information-theoretic approach. Second edition. Springer Science and Business Media, New York, USA.

Burton, R. 1995. National Audubon Society North American birdfeeder handbook. DK Publishing, Inc., New York, USA.

Cameron, A. C. and F. A. G. Windmeijer. 1996. R-squared measures for count data regression models with applications to health care utilization. Journal of Business and Economic Statistics 14:209–220.

Collins, K. A. and D. J. Horn. 2012. The role of oil content and size in seed selection by wild birds. Transactions of the Illinois State Academy of Science 105:107–117.

Díaz, M. 1990. Interspecific patterns of seed selection among granivorous passerines: effects of seed size, seed nutritive value and bird morphology. Ibis 132:467–476.

Díaz, M. 1996. Food choice by seed-eating birds in relation to seed chemistry. Comparative Biochemistry and Physiology Part A: Physiology 113:239–246.

Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen science as an ecological research tool: challenges and benefits. Annual Review of Ecology, Evolution, and Systematics 41:149–172.

Dunn, E. H. and D. L. Tessaglia-Hymes. 1999. Birds at your feeder: a guide to feeding habits, behavior, distribution, and abundance. W. W. Norton and Company, New York, USA.

Geis, A. D. 1980. Relative attractiveness of different foods at wild bird feeders. U.S. Fish and Wildlife Service Special Scientific Report No. 233. Department of the Interior, Washington, D.C., USA.

Harrison, K. and G. Harrison. 1983. America's favorite backyard birds. Simon and Schuster, New York, USA.

Hayslette, S. E. 2006. Seed-size selection in Mourning Doves and Eurasian Collared-Doves. Wilson Journal of Ornithology 118:64–69.

HAYSLETTE, S. E. AND R. E. MIRARCHI. 2001. Patterns of food preferences in Mourning Doves. Journal of Wildlife Management 65:816–827.

HEINRICH, B., C. C. JOERG, S. S. MADDEN, AND E. W. SANDERS. 1997. Black-capped Chickadees and Red-breasted Nuthatches "weigh" sunflower seeds. Auk 114:298–299.

HENKE, S. E., V. C. GALLARDO, B. MARTINEZ, AND R. BAILEY. 2001. Survey of aflatoxin concentrations in wild bird seed purchased in Texas. Journal of Wildlife Diseases 37:831–835.

HORN, D. J. 1999. The species richness of birds visiting a yard is influenced by the feeders/seeds present. Journal of the Iowa Academy of Science 106:21–25.

HORN, D. J., S. M. JOHANSEN, AND T. E. WILCOXEN. 2014. Seed and feeder use by birds in the United States and Canada. Wildlife Society Bulletin 38:18–25.

HRABAR, H. D. N. K. AND M. PERRIN. 2002. The effect of bill structure on seed selection by granivorous birds. African Zoology 37:67–80.

HRISTIENKO, H. AND J. E. MCDONALD. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. Ursus 18:72–88.

LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the Black-capped Chickadee. Oecologia 66:60–67.

PULLIAM, H. R. 1980. Do Chipping Sparrows forage optimally? Ardea 68:75–82.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.

RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, M. S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. H. DUNN, W. C. HUNTER, E. E. IÑIGO-ELIAS, J. A. KENNEDY, A. M. MARTELL, A. O. PANJABI, D. N. PASHLEY, K. V. ROSENBERG, C. M. RUSTAY, J. S. WENDT, AND T. C. WILL. 2004. Partners in flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, New York, USA.

RÍOS, J. M., A. MANGIONE, AND L. MARONE. 2012a. Effects of nutritional and anti-nutritional properties of seeds on the feeding ecology of seed-eating birds of the Monte Desert, Argentina. Condor 114:44–55.

RÍOS, J. M., A. M. MANGIONE, AND L. MARONE. 2012b. Tolerance to dietary phenolics and diet breadth in three seed-eating birds: implications for graminivory. Journal of Experimental Zoology 317:425–433.

SILVERTOWN, J. 2009. A new dawn for citizen science. Trends in Ecology and Evolution 24:467–471.

SPSS INSTITUTE INC. 2009. SPSS for Windows. Version PASW 17.0. SPSS Institute Inc., Chicago, Illinois, USA.

THUMBULL, D. J., R. BONNEY, D. BASCOM, AND A. CABRAL. 2000. Thinking scientifically during participation in a citizen-science project. Science Education 84:265–275.

U.S. FISH AND WILDLIFE SERVICE. 2012. 2011 national survey of fishing, hunting, and wildlife-associated recreation-National Overview.

VAN DER MEIJ, M. A. A., M. GRIEKSPOOR, AND R. G. BOUT. 2004. The effect of seed hardness on husking time in finches. Animal Biology 54:195–205.

WILLSON, M. F. 1972. Seed size preference in finches. Wilson Bulletin 84:449–455.

WILLSON, M. F. AND J. C. HARMESON. 1973. Seed preferences and digestive efficiency of cardinals and Song Sparrows. Condor 75:225–234.

The Wilson Journal of Ornithology 126(2):381–388, 2014

Nesting of Laughing Falcons (*Herpetotheres cachinnans*) in the Pantanal, Brazil, with Remarks on Young Plumage and Nestling Vocalization

Karlla V. C. Barbosa,[1,4,6] Thiago Filadelfo,[1,2] Monalyssa Camandaroba,[1,3] Thiago V. V. Costa,[4] and Neiva M. R. Guedes[1,5]

[1] Hyacinth Macaw Project, Instituto Arara Azul, Rua Klaus Sthurk, 178, Jardim Mansur, CEP 79051-660, Campo Grande, MS, Brazil.

[2] Universidade de Brasília, Campus Universitário Darcy Ribeiro, CEP 70910-900, Brasília, DF, Brazil.

[3] Al Wabra Wildlife Preservation, Qatar.

[4] Museu de Zoologia da Universidade de São Paulo, Avenida Nazaré 481, Ipiranga, CEP 04263-000, São Paulo, SP, Brazil.

[5] Universidade Anhanguera Uniderp, Post-Graduation Program in Environment and Regional Development, Rua Ceará, 333, Miguel Couto, CEP 79003-310, Campo Grande, MS, Brazil.

[6] Corresponding author;
e-mail: barbosa.karlla@gmail.com

ABSTRACT.—Laughing Falcons (*Herpetotheres cachinnans*) are common, medium-sized falconids that occur throughout the Neotropical region and marginally in the Nearctic American continent. There is little data on their breeding biology with the only information available based on scattered records. Here, we report data on 11 nests of *H. cachinnans* from the Pantanal, Brazil, including four in nest-boxes, between 2007–2008. The breeding season occurred between July–December, which is in accordance with the few records for this region. Records of two eggs or nestlings were found in 28% ($n = 3$) of nests, while the remaining 72% ($n = 8$) had one egg or nestling. The eggs were rounded and buff with brown markings or dark brown or purplish

brown with darker markings. The hatchlings, even when a few days old, are pale buff overall in plumage with the distinctive black mask, typical of the adults. An undescribed vocalization of the nestling was recorded, which is similar to an uncommon vocal type emitted by the adults when disturbed. The study reveals novel data on the use of nest-boxes and on the breeding biology of the species, and reinforces the importance of such studies on its conservation. *Received 26 July 2013. Accepted 30 November 2013.*

Key words: breeding biology, cavity, Falconidae, *Herpetotheres*, nest-box, nesting.

Laughing Falcons (*Herpetotheres cachinnans*) are widespread falconids that occur in the Neotropical region and marginally in the Nearctic American continent. In Brazil they are encountered throughout the country, with a few scattered records in the extreme southern part of their distribution (White et al. 1994, Ferguson-Lees and Christie 2001). They are medium-sized falcons, weighing ~600 g (male) to 700 g (female), and are characterized by a white or pale buff plumage overall, brown wings, a tail with three or four buff bands, and a large head with a distinctive black mask extending from the eyes to the nape, traits that make the species unmistakable (White et al. 1994, Ferguson-Lees and Christie 2001, Parker et al. 2012). In spite of being widespread and considered common throughout most of their range, they can be considered rare and even in decline in some regions (White et al. 1994, Ferguson-Lees and Christie 2001), perhaps because of a decline of their specialized diet, composed primarily of snakes, venomous (e.g., *Micrurus* spp., *Crotalus durissus*) and non-venomous (Wetmore 1965, Ferguson-Lees and Christie 2001, DuVal et al. 2006, Specht et al. 2008), and/or because of reduced availability of cavities for nesting that may limit their success in areas with high human disturbance (Wetmore 1965).

The breeding season of this species may vary across its distribution, occurring in April in Mexico, February in Guatemala south to Costa Rica and January in northern Argentina (White et al. 1994). In Brazil, the breeding biology of the species is poorly known – one nest was reported with nestlings in September (Specht et al. 2008). The species nests in cavities or depressions, placed in somewhat exposed situations, either in an isolated tree or above the height of the surrounding vegetation (Parker et al. 2012). One or two eggs are laid, and the female does all the incubating, though both parents take care of the nestlings. Nestlings leave the nest 50–59 days after hatching (Skutch 1999, Ferguson-Lees and Christie 2001, Parker et al. 2012).

The vocal repertoire of the species is composed by a variety of different songs and calls. In general, the species delivers mostly short nasal laughing calls and a full advertisement song consisting of a long, rhythmic, broadcasting series that can last >9 min when a pair is duetting (Ferguson-Lees and Christie 2001). Few data exist concerning vocalizations of juveniles or nestlings, but some calls are reported for nestlings from the second week after hatching (Parker et al. 2012).

Here, we present new data on the breeding biology of *Herpetotheres cachinnans* based on eleven nests from the southern Pantanal near Miranda, Brazil, and provide novel data on the use of nest-boxes by the species, as well as details on the eggs, nestlings, plumage of the juveniles, and an undescribed vocalization of nestlings.

METHODS

Study Area.—The data presented here were collected in the Pantanal region, at the Refúgio Ecológico Caiman (19° 51′–19° 58′ S, 56° 17′–56° 24′ W) and nearby localities, in the municipality of Miranda, State of Mato Grosso do Sul, Brazil (Fig. 1). The region is located in the Cerrado domain (Ab'Saber 2003), and represents a mosaic of habitats which includes different vegetation types, such as *Cerrado stricto sensu* (savanna woodland, with trees reaching up to 7 m high), gallery-forests, grasslands, open areas, and the typical *Capões* or *Cordilheiras,* which consist of large woodlots of tall *Cerrado* forest, situated close to aquatic habitats such as saline lakes and freshwater lagoons (Eiten 1991, Harris et al. 2005).

Data Collection.—The data presented here were collected under the auspices of the Hyacinth Macaw Project, which has been monitoring nests of Hyacinth Macaw (*Anodorhynchus hyacinthinus*) in the Pantanal region, mainly in the state of Mato Grosso do Sul, since 1990 (Guedes 2004a). One aspect of the project has been to provide artificial nests for the Hyacinth Macaws, in order to mitigate a possible shortage of natural nest cavities for the species. In addition to *A. hyancinthinus*, these artificial nests have been used by 17 bird species, including *H. cachinnans* (Guedes 2004b). The wooden nest-boxes are rectangular in structure and measure 40 × 50 × 60 cm, with a circular entrance 15 cm wide. The

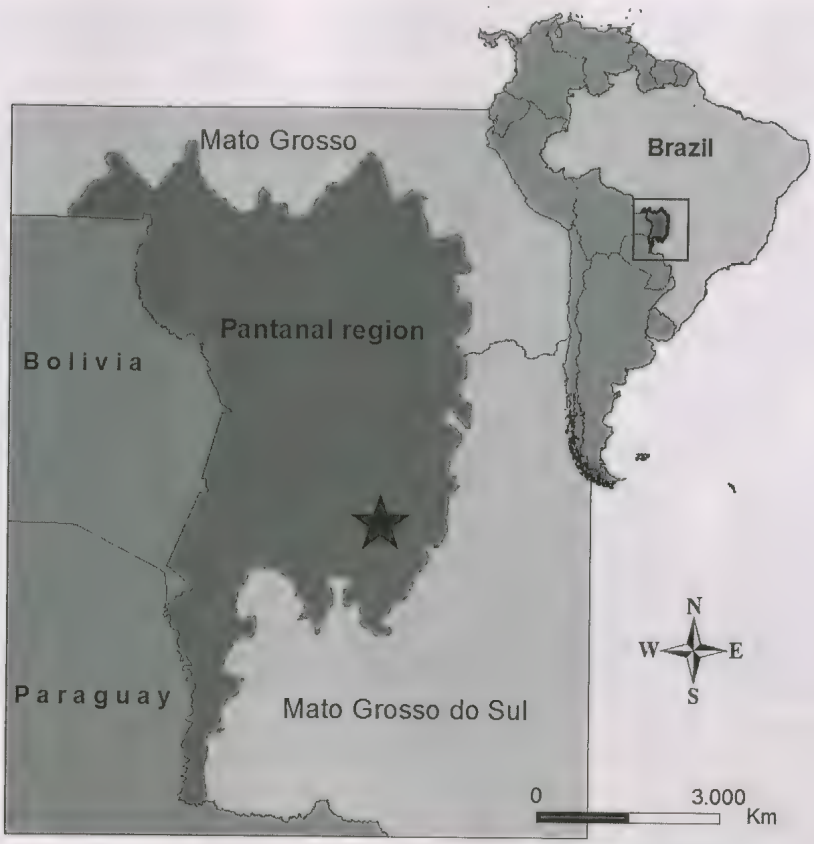


FIG. 1. Map depicting the region of the Brazilian Pantanal, on the border Brazil-Bolivia-Paraguay. Star represents the study area where the nests of Laughing Falcons were monitored, in the Pantanal, Mato Grosso do Sul, Brazil.

floor of the nest-boxes are covered with wood-chips and installed in large trees (see Guedes 2008 for more details on the project and the artificial nests). Between 2007–2008, we monitored natural cavities previously known to be occupied by Hyacinth Macaws during the reproductive season, which occurs mostly between July–December. The nests were monitored on average once a month with observations made using binoculars and by climbing trees using ascending and rappelling techniques. The nests, eggs, nestlings, and juveniles were photographed with digital cameras SONY DSC-P73 and NIKON E4600. Vocalizations of a nestling were extracted from a video recording and corresponding spectrograms produced using Adobe Audition 3.0 and MS Photoshop. The recording is available at Xeno-Canto.org under the access number 126969.

RESULTS AND DISCUSSION

We found a total of 11 nests occupied by Laughing Falcons - seven natural cavities and four artificial nests (information about each nest is depicted in Table 1; Fig. 2). All nests were found between early July–December and one of them was occupied in 2007 and 2008. This result is in accordance with a nest reported in southeastern Brazil, which was recorded between early September and late October (Specht et al. 2008).

All the Laughing Falcons' nests, both natural cavities and nest-boxes, reported here were also previously used by Hyacinth Macaws. The nests were in big trees surrounded by vegetation in the typical *capões* or *cordilheiras*, with one nest recorded on the border of a *cordilheira*, close to a pasture, in a nest-box installed on a Braúna tree (*Schinopsis brasiliensis*). Most of the natural cavities were found in Manduvi trees (*Sterculia apetala*, Fig. 2a), a species known to host more than 95% of the Hyacinth Macaws' nests (Guedes and Harper 1995). In the Pantanal, this tree grows in natural forest fragments, *cordilheiras* and *capões*, and in order to be able to provide a potential cavity nest, it needs to be older than

TABLE 1. Information about Laughing Falcons' nests, eggs, and nestlings found 2007–2008 in the Pantanal, Mato Grosso do Sul, Brazil. Id: nest identification; N: internal Id number of the Hyacinth Macaw Project; Type: NC = Natural cavity or AN = Artificial nest; T1: First time of monitoring; stage: egg (e), nestling (n), young (y) or egg depredated (†); T2: Second time of monitoring; LT: Last day of monitoring the nest.

Id	N	Type	T1	Stage	T2	Stage	LT	Stage	Observation
2007									
N1	355	NC	09 August	1e	12 September	†	–	–	Occupied by Hyacinth Macaw on 12 September
N2	211	NC	10 September	1e	05 October	1n	30 October	1y	On 10 December the nest was empty
N3	237	NC	14 September	1e	27 September	1e	08 November	†	Occupied by Collared Forest-Falcon on 8 November
N4	2112	AN	27 October	1e	03 December	1e	13 December	1n	–
N5	207	NC	05 November	1e	12 December	†	–	–	Nest empty on 12 December
N6	245	NC	September	1e	October	†	–	–	Precise day of T1 not known
2008									–
N7	183	NC	28 August	0	03 November	1n	13 November	–	On 28 August the adult was inside the nest
N8	366	NC	25 July	2e	16 September	2n	–	–	On 10 November the nestlings were gone and the nest was occupied by *Ramphastos toco*
N9	2096	AN	04 September	2e	16 September	†	–	–	Precise day of the death not known
N10	2112	AN	03 September	1e	19 September	1e	14 October	1n	On 30 November the nest was empty
N11	2139	AN	22 October	2e	10 November	2n	–	–	On 29 November the nest was empty

FIG. 2. Nests of Laughing Falcon (*Herpetotheres cachinnans*) in the Pantanal, Brazil. A – Natural nest (N8) active in 2007; B – Artificial nest occupied in 2007 (N4) and 2008 (N10).

60 years and reach a diameter at breast height of more than 70 cm (Santos et al. 2006).

From the 11 nests monitored, eight nests had one egg or nestling, while only three had two eggs or nestlings, totaling 14 eggs. The eggs were rounded and buff with brown markings, dark brown or purplish brown with darker markings (Fig. 3), and one egg studied weighed 60 g, measured 56.7 mm in length and 44.3 mm in width, much like what has been observed in others studies (Wolfe 1954, Skutch 1999, Specht et al. 2008). The color patterns of the eggs are slightly different from that reported by other authors, who mention them as being white with a great amount of medium-sized dark brown spots (Wolfe 1954, Specht et al. 2008). The dark purple coloration of some eggs observed is very similar to those of Collared Forest-Falcon (*Micrastur semitorquatus*) as reported in the literature and observed on other occasions at the study site (Barbosa et al. 2014). The clutch size varied from 1–2 eggs/nestlings, as already suggested in the literature (Wolfe 1954, Skutch 1999, Ferguson-Lees and Christie 2001), but in 72% of the nests ($n = 8$) only one egg or nestling was observed, as in some known studies (Skutch 1999, Miller et al. 2010). Many factors have been already mentioned as influencing clutch size in different groups of birds, including latitude and prey availability, among others (Jetz et al. 2008). Based on our data, we can infer that latitude does not appear to influence clutch size in *H. cachinnans*, but other factors, such as prey availability or type, may have an effect.

From the 11 nests recorded, six were found in the breeding season of 2007 and five in 2008. One of the artificial nests (N 2112) found in 2007 was reoccupied by the species in the following year, possibly by the same pair. Among the 11 nests, roughly 45% ($n = 5$) were depredated while as eggs. The remaining nests consisted of four nests with one nestling each and two nests with two nestlings each.

On 7 August 2007, when monitoring nest N3 a couple of Laughing Falcons were observed defending the nest, which upon inspection was empty. Thirty-eight days later, on 14 September, only one adult individual was present and one egg was inside the nest. Thirteen days later, on 27 September, the egg was observed to be intact and an adult individual was present nearby the nest. However, 42 days later on 8 November, the egg was gone and an adult Collared Forest-Falcon had occupied the nest and laid two eggs. In the Pantanal, these species compete with each other for cavities and with other species, such as

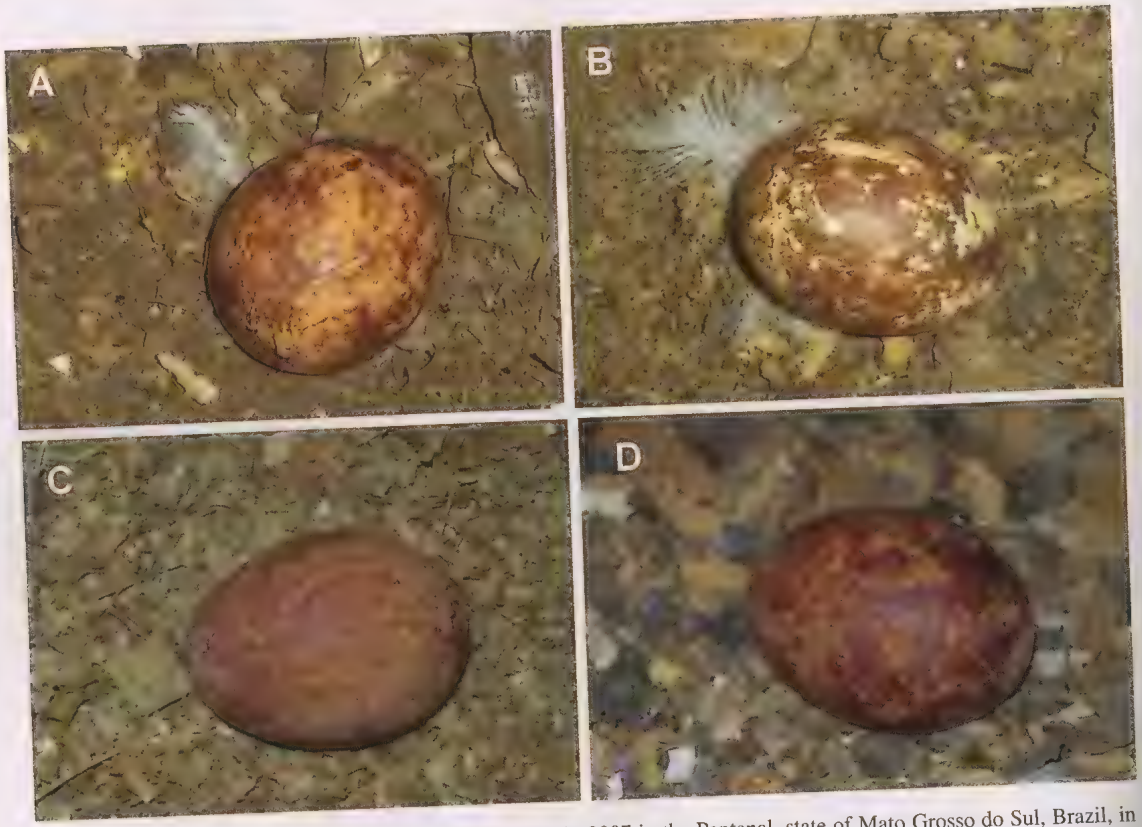


FIG. 3. Eggs of Laughing Falcon from nests recorded in 2007 in the Pantanal, state of Mato Grosso do Sul, Brazil, in different nests and months: A (N1) August; B (N3) September; C (N4) October; D (N5) November.

Hyacinth Macaws (Guedes 2004b, Barbosa et al. 2014).

The nestlings observed were very similar in plumage to each other, with the body and wings covered in pale buff plumes, and their distinctive black face masks already evident (Fig. 4A). In one of the nests monitored, a nestling ~1 month old was just a little larger and very similar to the first plumage observed, consisting of pale buff overall, but with brownish wing coverts and dark thin stripes in the head (Fig. 4C). We were not able to check that nest in the following weeks and in the last observations, roughly 1 month later, the young was not in the nest anymore and no adults were seen. We are unable to determine the fate of this nest, though it is plausible the nestling fledged.

Four of the eleven clutches were located in nest-boxes. In one of them (N4), we found an egg on 27 October 2007 with the parents close by and vocalizing actively (Fig. 3C). On 3 December, the egg was still there and the parents were present nearby. Ten days later, we recorded a nestling about 3–4 days old, which was photographed and had its vocalization recorded. The calls recorded from this nestling may represent an undescribed vocalization of the species. The calls consisted of short phrases composed of 6–10 notes, lasting 1.5–2 secs, slightly descending in frequency and repeated randomly (Fig. 5). All the single notes varied from 0.5–1 kHz in frequency and 0.1 secs in time, except the first note which is more than two times longer and slightly higher in frequency than the rest. This vocalization is somewhat similar to that emitted by adults when under threat, as they felt on the occasions when we were present nearby their nests. It also consists of short phrases, lasting about 2 sec, composed by roughly 10 notes slightly descending in frequency and with the first note longer and higher in frequency than the remaining (KVCB, pers. obs.). In spite of the similarity between the vocalization of the nestling and the adult and that both are observed when the birds are under some threat, it is still unknown if they are delivered in the same behavioral context. A few other vocalizations have been reported for Laughing Falcon chicks, all of them coming from chicks 2 weeks old or older. Apparent food begging

FIG. 4. Nestlings of Laughing Falcon (*Herpetotheres cachinnans*) from natural nests in the Pantanal, Mato Grosso do Sul, Brazil. A and C: October 2007 (N2); B: July 2008 (N8).

calls, cackle calls during handling and a soft "wah" call were delivered by chicks from 15–40 days old (Parker et al. 2012). However, there is no mention in the literature of the vocalization type we report here, or from chicks of such an early age (3–4 days old).

From the seven natural nests, four were seemingly depredated (N1, N3, N5 and N6), as the eggs disappeared without any sign or remains found. Thus, from the seven nests recorded, only three were successful. The fact that the species breeds only once a year and lays 1–2 eggs each time (White et al. 1994, Specht et al. 2008) and may compete for nest cavities also highlights the importance of the use of nest-boxes in the reproduction of the species.

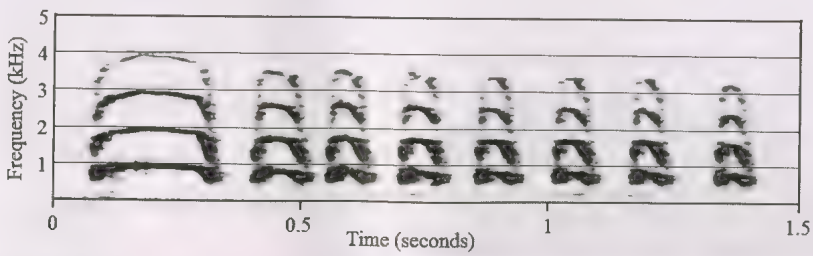


FIG. 5. Spectrogram of the vocalization delivered by the nestling of Laughing Falcons in the Pantanal, Brazil. The recording is available at Xeno-Canto.org under access number 126969.

The results presented here reveal new information on the breeding biology of Laughing Falcons, refining the proximal dates of the breeding season of the species in the Pantanal region, providing new descriptions of egg coloration, new information concerning the plumage of the young and a noteworthy, possibly undescribed vocalization of a nestling. From a conservation perspective, this study stresses the importance of monitoring nests of cavity-nesting birds, especially of those experiencing population declines.

Although reports exist of Laughing Falcons using nest-boxes for nesting (Guedes 2004b), this paper provides novel and detailed data on the breeding biology of the species and indicates that Laughing Falcons may successfully reproduce in such nests. Our data also reinforce the importance of large, natural cavities for the reproduction of many bird species and, furthermore, highlight the potential importance of artificial nests, such as nest-boxes, as a conservation tool in situations where there is a genuine shortage of available cavities for nesting.

ACKNOWLEDGMENTS

We are indebted to the Hyacinth Macaw Project partners, especially to Universidade Anhanguera Uniderp, Fundação Toyota do Brasil, Refúgio Ecológico Caiman, Parrots International and Bradesco Capitalização. We also thank all our collaborators for their support, particularly to C. C. Corrêa and E. R. Guedes for their valuable help during the fieldwork. We are also very grateful to R. Watson, M. B. Brown and two anonymous reviewers for their valuable suggestions and comments on the manuscript.

LITERATURE CITED

Ab'Saber, A. N. 2003. Os domínios de natureza no Brasil: potencialidades paisagísticas. Ateliê Editorial, São Paulo, Brasil.

Barbosa, K. V. C., T. Filadelfo, and N. M. R. Guedes. 2014. Artificial incubation and introduction of a Collared Forest-Falcon chick (*Micrastur semitorquatus*) into a natural nest in Southern Pantanal, Brazil. Revista Brasileira de Ornitologia. 22:22–26.

Duval, E. H., H. W. Greene, and K. L. Manno. 2006. Laughing Falcon (*Herpetotheres cachinnans*) predation on coral snakes (*Micrurus nigrocinctus*). Biotropica 38:566–568.

Eiten, G. 1991. Vegetação do Cerrado. Pages 9–65 *in* Cerrado, caracterização, ocupação e perspectivas (M. N. Pinto, Editor). Editora Universidade de Brasília, Brasília, Brazil.

Ferguson-Lees, J. and D. A. Christie. 2001. Raptors of the world. Houghton Mifflin Company, New York, USA.

Guedes, N. M. R. 2004a. Management and Conservation of the large macaws in the wild. Ornitologia Neotropical 15:279–283.

Guedes, N. M. R. 2004b. Araras azuis: 15 anos de estudo no Pantanal. Pages 1–12 *in* IV Simpósio sobre recursos naturais e sócio-econômico do Pantanal. Corumbá, MS, Brazil.

Guedes, N. M. R. 2008. Projeto para confecção de ninhos artificiais para Arara-azul. Instituto Arara Azul, Campo Grande, Brasil. www.projetoararaazul.org.br (accessed 14 Mar 2013).

Guedes, N. M. R. and L. H. Harper. 1995. Hyacinth Macaw in the Pantanal. Pages 394–421 *in* The large macaws: their care, breeding and conservation (J. Abramson, B. L. Spenn, and J. B. Thomsen, Editors). Raintree Publications, London, UK.

Harris, M. B., W. B. Tomas, G. Mourão, C. J. Silva, E. Guimarães, F. Sonoda, and E. Fachim. 2005. Desafios para proteger o Pantanal Brasileiro: ameaças e iniciativas em conservação. Megadiversidade 1:156–164.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS Biology 6:2650–2657.

Miller, E. T., H. F. Greeney, and U. Valdez. 2010. Breeding behavior of the Laughing Falcon (*Herpetotheres cachinnans*) in southwestern Ecuador and northwestern Peru. Ornitología Colombiana 10:43–50.

Parker, M. N., A. M. Enamorado, and M. Lima. 2012. Laughing Falcon. Pages 265–280 *in* Neotropical birds of prey: biology and ecology of a forest raptor community (D. F. Whitacre, Editor). Cornell University Press, Ithaca, NY, USA.

Santos Jr., A., I. H. Ishii, N. M. R. Guedes, and F. L. R. Almeida. 2006. Appraisal of the age of the trees used as nest by the Hyacinth Macaw in the Pantanal, Mato Grosso. Natureza & Conservação 4:180–188.

Skutch, A. F. 1999. Trogons, Laughing Falcons, and other Neotropical birds. Texas A&M University Press, College Station, USA.

Specht, G., E. P. Mesquita, and F. A. Santos. 2008. Breeding biology of Laughing Falcon *Herpetotheres cachinnans* (Linnaeus, 1758) (Falconidae) in southeastern Brazil. Revista Brasileira de Ornitologia 16: 155–159.

Wetmore, A. 1965. The birds of the Republic of Panama. Smithsonian Institution, Washington D.C., USA.

White, C. M., P. D. Olsen and L. F. Kiff. 1994. Family Falconidae (Falcons and Caracaras). Pages 216–256 *in* Handbook of the birds of the world. Volume 2. New World Vultures to Guineafowl (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

Wolfe, L. R. 1954. Nesting of the Laughing Falcon. Condor 56:161–162.

The Wilson Journal of Ornithology 126(2):389–392, 2014

First Nest Record of Red-throated Caracara (*Ibycter americanus*) for Middle America

Ruth E. Bennett,[1,7] Isidro Zuniga,[2] Mark Bonta,[3] David L. Anderson,[4] Sean McCann,[5] and Luis Herrera[6]

ABSTRACT.—Populations of Red-throated Caracaras (*Ibycter americanus*) have been extirpated or are in serious decline throughout Middle America. We describe the first nest outside South America and provide only the third nest description for the species. We observed four adults and one immature Red-throated Caracara provide cooperative care to a single nestling at a nest in a region dominated by pine-oak forest in departamento (dpto.) de Olancho, Honduras. The nest was a bowl-shaped structure of branches and pine needles located at the mid-canopy level of a pine tree (*Pinus oocarpa*), and is the first nest described in an ecosystem other than humid broadleaf forest. We report the first observation of adult Red-throated Caracaras using a nest as a short-term food cache, as well as the first observation of Red-throated Caracara taking fledgling birds as prey. Although Red-throated Caracaras are considered a resident of humid broadleaf forest, we suggest that pine-oak forests may be an important habitat for the species in the northern portion of its range. *Received 31 October 2013. Accepted 7 December 2013.*

Key words: Honduras, *Ibycter americanus*, nest, pine forest, Red-throated Caracara.

Although formerly widespread from southern Mexico to the Amazon Basin, populations of Red-throated Caracaras (*Ibycter americanus*) have plummeted over much of the species' range since the mid-20th century (Bierregaard 1994, Ferguson-Lees and Christie 2001). The species appears to have been extirpated from the northernmost portion of its range, from Chiapas and southern Veracruz, Mexico, through the Pacific Coast of Guatemala (Land 1970, Ceballos and Marquez Valdelamar 2000). In Honduras, the species has disappeared from most of its former range along the Atlantic slope and portions of the interior (Monroe 1968, Bonta 2003). Similar declines have been reported in Costa Rica and Panama (Ridgely and Gwynne 1989, Stiles and Skutch 1989). The majority of the South American range, consisting primarily of the Amazon Basin south to Atlantic coastal Brazil, supports a robust population. However, regional extirpation has occurred on the Pacific slope of Ecuador and Colombia (Ferguson-Lees and Christie 2001, Ridgely and Greenfield 2001). Red-throated Caracaras are known to be associates of primary evergreen broadleaf forest and to a lesser extent tropical dry forest and forest edges (Monroe 1968, Bierregaard 1994, Ceballos and Marquez Valdelamar 2000). The current decline in Middle America is perplexing, because the species seems to have disappeared from large tracts of seemingly suitable, intact forest (Ridgely and Gwynne 1989).

The northern population of Red-throated Caracaras, which formerly occurred from Mexico through southern Costa Rica, has been described as a separate taxonomic unit, *I. a. guatemalensis*, because individuals have consistently longer body and wing lengths than in the southern population (Swann 1921, Wetmore et al. 1965). The taxonomic status of the northern population remains unresolved however (Bierregaard 1994), and little is known about the current size and viability of the northern population. Scattered and irregular reports from Honduras southward indicate that *I. a. guatemalensis* persists in small, geographically isolated populations (Stiles et al. 1989, Anderson et al. 2004, Narish and Jenner 2004), but breeding has never been documented in the region.

On 12 March 2013, we observed a group of five Red-throated Caracaras exhibiting courtship behavior in departamento (dpto.) de Olancho, Honduras. We recorded copulation on 20 March

[1] Department of Natural Resources, Cornell University, Ithaca, NY 14850, USA.
[2] Finca Las Orquídeas, El Ocotal, Gualaco, Olancho, Honduras.
[3] Division of Mathematics and Natural Sciences, Penn State Altoona, 3000 Ivyside Park, Altoona, PA 16601, USA.
[4] The Peregrine Fund, 5668 W. Flying Hawk Lane, Boise, ID 83709, USA.
[5] Department of Biological Sciences, Simon Fraser University, Burnaby BC, Canada.
[6] Jaguar Program, Panthera, 3425, Bloque M, Los Robles, Tegucigalpa, Honduras.
[7] Corresponding Author; e-mail: reb349@cornell.edu

between two birds and subsequently discovered a nest on 17 April. The nest site occurred within a pine-oak ecosystem characterized by sparse forest with an overstory of pine (*Pinus oocpara*), midstory of oak (*Quercus* spp.), and understory of grasses and shrubs. This forest type stretches across the north of dpto. de Olancho at elevations between 600–1300 m in areas with high topographic relief. These forests are subject to yearly burning, which local residents use to control shrubs and promote grass regeneration for cattle grazing. The nearest extensions of humid evergreen broadleaf forest lie 12 km to the southwest and 16 km to the north. Broadleaf forest generally occurs at elevations above 1,300 m in areas with higher levels of annual rainfall and more productive soils. Presence of a contiguous broadleaf canopy, lianas, and an herbaceous understory distinguish broadleaf forest from pine-oak forest.

METHODS

We monitored the nest for 18 days between 17 April–23 May when the nestling fledged. Observations were made each day from 0430–1630 CST, which covers the entire daily time span during which the Red-throated Caracaras were active. All observations were made with 8 × 42 binoculars from a blind 100 m upslope from the nest. Behavior and food deliveries were recorded with a Canon Powershot SX40 camera. The following information is based on a total of 312 hrs of observation at this nest.

OBSERVATIONS

The nest was a loose platform located 16 m above ground on the lowest branch of a 37-m tall pine tree (*P. oocarpa*) with a diameter at breast height of 56 cm. The nest structure was bowl-shaped, measuring ~1 m wide and 0.5 m deep. The bowl consisted of compacted pine needles and Spanish moss (*Tillandsia* sp.) packed around a dense cluster of pine branches measuring 1–20 cm in diameter. We were unable to discern if caracaras or another large bird had constructed the nest, or if it was a naturally occurring basin of fallen needles on a branch cluster. The nest was located in the tallest tree within a 20-m radius on a south-facing hill with a 40-degree slope at 860 masl. Pine (*P. oocarpa*) dominated the overstory of the forest, and a mixture of oak (*Quercus* spp.) and regenerating pine comprised the mid-story. The understory was devoid of herbaceous vegetation because of a human-induced fire that burned through the area three days before the nest was discovered.

TABLE 1. Composition of food items brought to a nest of Red-throated Caracara in pine-oak forest, dpto. de Olancho, Honduras, 17 April–23 May 2013.

Food Item	Number (% of total)
Wasp brood comb	169 (80.9)
Unidentified	30 (14.3)
Order Coleoptera	6 (2.9)
Birds (fledglings or nestlings)	3 (1.4)
Spider egg sac	1 (0.5)
TOTAL	209 (100.0)

Four adults and one immature Red-throated Caracara cooperatively attended the nest. Individuals were aged using plumage characteristics (Ferguson-Lees and Christie 2001). The immature had noticeable molt limits on flight feathers and coverts, possessed a shorter tail than adults with notable wear, and had pale red facial skin. The four adults possessed dark red facial skin and basic plumage without noticeable molt. Because none of the caracaras were marked, it was not possible to assess differences in amount of care provided by individual adults. However, the immature caracara provided noticeably less care than the adults, acting as sentinel on two occasions and bringing food into the nest on three occasions.

Red-throated Caracaras became active each day between 0449–0525 and ended activity between 1753–1818. During the observation period, the sun rose between 0516–0531 and set between 1802–1812; thus the active period began ~10 mins before sunrise and ended at sunset. At night, one adult roosted in the nest while the other four individuals roosted 200–500 m away. During the day, one adult remained within 100 m of the nest, aggressively defending it against other bird species and the observer, if he was detected. We observed only two instances where the nestling was left alone, once for two hrs during a morning and once overnight. While one caracara acted as a sentinel, the other four individuals foraged and periodically returned to the nest with food items.

During the entire 18-day observation period, we documented 379 nest visits made by single caracaras ($\bar{x}$ = 17/day) of which 208 involved a food delivery ($\bar{x}$ = 10/day). Pieces of wasp brood comb comprised over 80% of the food items delivered (Table 1). At least three prey items were nestling or fledgling birds. We did not

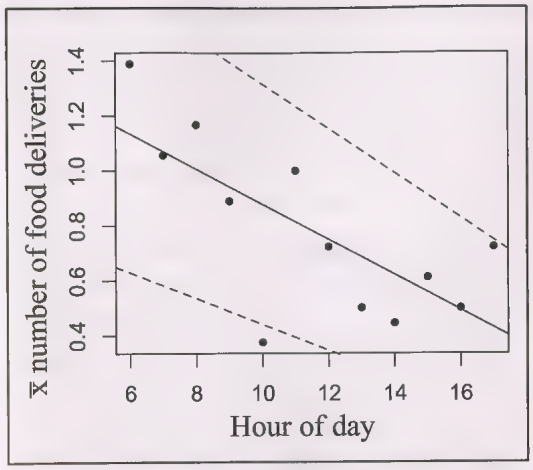


FIG. 1. Mean number of daily food deliveries per hour of day. $P = 0.008$, $r^2 = 0.48$. Dotted lines show 95% CI.

document any deliveries of fruit, which are an important food source for Red-throated Caracara in South America (Thiollay 1991, McCann et al. 2010).

Food-deliveries were short in duration; 74% lasted <1 min, and deliveries decreased in frequency throughout the day (Fig. 1). In contrast, 73% of nest visits that did not involve a food delivery lasted >1 min, with adults spending a cumulative 42 min/day (SD = 8 min) in the nest with the nestling. On three of these occasions, we observed the sentinel adult enter the nest without food and feed the chick larvae that it removed from previously deposited wasp brood combs. These observations suggest that foraging adults cache food in the nest, particularly in the morning when they deposit the majority of food items, and that the sentinel bird feeds the nestling from the cached food.

Because of the bowl-like structure of the nest, we were unable to observe the nestling's development until 1 May, when it had ~7.5-cm long primary feathers and was capable of flapping and walking. By this date, the chick was well beyond the developmental stage of a 22-day old nestling as documented by McCann et al. (2010). On 25 May, we observed a nestling caracara flying 1.5 km from the nest site, and presume successful fledging from the nest. We can assume that the nestling period was at least 47 days, similar to the 57-day period proposed by McCann et al. (2010).

DISCUSSION

The breeding biology of Red-throated Caracaras remains poorly known. Although our observations confirm communal nest guarding and brood care of a single young, as has been documented previously (Thiollay 1991, Whittaker 1995, McCann et al. 2010), our observations expand the current knowledge of this species' biology in several regards. Unlike McCann et al. (2010), we did not observe any fruit or millipedes delivered to the nest. We report the first observation of avian prey in the diet of Red-throated Caracaras, which along with a single report of lizards recovered from a Mexican bird (Lowery and Dalquest 1951) are the only vertebrate prey reported for this species. Our

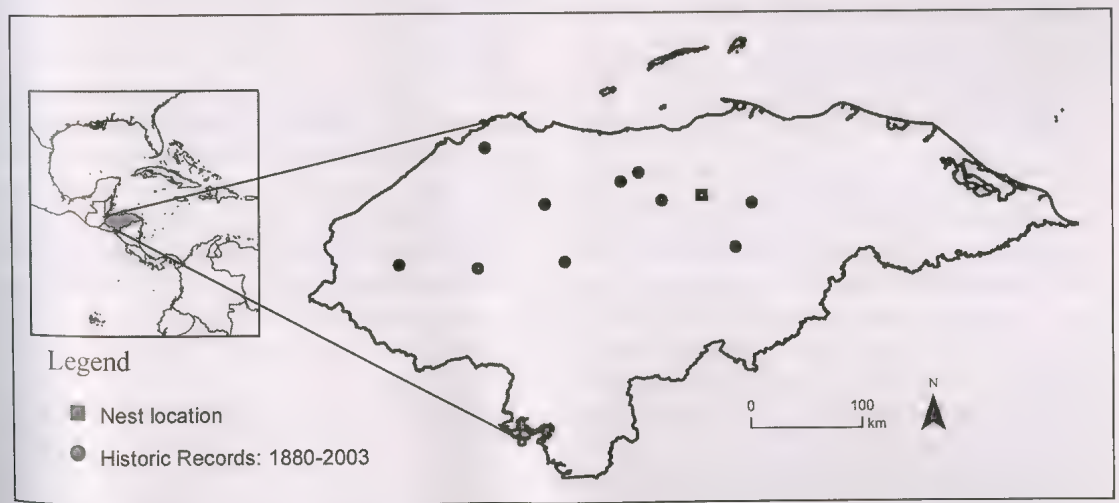


FIG. 2. Map of nest site and historic records of Red-throated Caracaras in Honduras. Historic records were compiled from Monroe (1968), Narish and Jenner (2004), and Moore Laboratory of Ornithology (2013).

observations of food caching expand our understanding of cooperative nestling care.

Knowledgeable local informants have reported a steep decline in the Red-throated Caracara population across dpto. de Olancho since 1980 (Bonta 2003). Given the absence of verified reports from other parts of Honduras where the species occurred formerly, it is unlikely that the species persists in the country outside of the pine-oak ecosystem centered in the northern dpto. de Olancho. The discovery of a nest in pine-oak forest challenges the assumption in Monroe (1968) that Red-throated Caracaras are restricted to humid broadleaf forest. In fact, all known museum specimens from Honduras were collected from the interior of the country, from dpto. de Lempira in the west to dpto. de Olancho in the east, where pine-oak forest dominates the mid-elevation landscape (Fig. 2). Our discovery of a cooperative group of five individuals caring for a nest in a pine-oak forest provides new evidence of the importance of conserving this ecosystem, which is highly threatened by logging, mining, road-building, and uncontrolled human-set fires.

ACKNOWLEDGMENTS

This research was funded by a grant from The Peregrine Fund. We would also like to thank Elvin Munguía, David Medina, Instituto Nacional de Conservación y Desarrollo Forestal, Areas Protegidas y Vida Silvestre (ICF), Rafael Ulloa, GIZ Prorena, and local community members across the region for their assistance with field observations and logistics.

LITERATURE CITED

ANDERSON, D. L., D. A. WIEDENFELD, M. J. BECHARD, AND S. J. NOVAK. 2004. Avian diversity in the Moskitia region of Honduras. Ornitologia Neotropical 15:447–482.

BIERREGAARD, R. O., JR. 1994. Species accounts of 81 species of Central and South American Falconiformes. Page 249 *in* Handbook of birds of the world. Volume 2. (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

BONTA, M. 2003. Seven names for the bellbird: conservation geography in Honduras. Texas A&M University Press, College Station, USA.

CEBALLOS, G. AND L. MÁRQUEZ VALDELAMAR (Editors). 2000. Las Aves de México en Peligro de Extinción. Instituto de Ecologia, D.F., Mexico.

FERGUSON-LEES, J. AND D. A. CHRISTIE. 2001. Raptors of the world. Houghton Mifflin Harcourt, New York, USA.

LAND, H. C. 1970. Birds of Guatemala. Livingston Publishing Company Wynnewood, Pennsylvania, USA.

LOWERY, G. H. AND W. W. DALQUEST. 1951. Birds from the state of Veracruz, Mexico. Volume 3. University of Kansas Publications, Lawrence, Kansas, USA.

MCCANN, S., O. MOERI, T. JONES, S. O'DONNELL, AND G. GRIES. 2010. Nesting and nest-provisioning of the Red-throated Caracara (*Ibycter americanus*) in central French Guiana. Journal of Raptor Research 44:236–40.

MONROE, B. L. 1968. A Distributional Survey of the Birds of Honduras. Ornithological Monograph 7. American Ornithologists' Union, Washington D.C., USA.

MOORE LABORATORY OF ZOOLOGY. Ornis2 Portal. ornis2.ornisnet.org (accessed 20 Oct 2013).

NARISH, A. J. AND T. JENNER. 2004. Notes on the Red-throated Caracara *Ibycter americanus* in Honduras. Cotinga 22:100.

RIDGELY, R. S. AND P. J. GREENFIELD. 2001. The birds of Ecuador: status, distribution, and taxonomy. Volume 1. Cornell University Press, Ithaca, New York, USA.

RIDGELY, R. S. AND J. A. GWYNNE. 1989. A guide to the birds of Panama: with Costa Rica, Nicaragua and Honduras. Princeton University Press, Princeton, New Jersey, USA.

STILES, F. G. AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, New York, USA.

SWANN, H. K. 1921. A Synopsis of the Accipitres (Diurnal Birds of Prey). Wheldon and Wesley Ltd., London, UK.

THIOLLAY, J. M. 1991. Foraging, home range use and social behavior of a group-living rainforest raptor, the Red-throated Caracara *Daptrius americanus*. Ibis 133:382–393.

WETMORE, A., R. F. PASQUIER, S. L. OLSON, AND D. C. SIEGEL. 1965. The birds of the Republic of Panama. Part 1. Smithsonian Institution, Washington, D.C., USA.

WHITTAKER, A. 1995. Nesting records of the genus *Daptrius* (Falconidae) from the Brazilian Amazon, with the first documented nest of the Black Caracara. Ararajuba 4:107–109.

The Wilson Journal of Ornithology 126(2):393–401, 2014

Breeding Biology of Squacco Herons (*Ardeola ralloides*) in Northern Tunisia

Aymen Nefla,[1,3] Wided Tlili,[1] Ridha Ouni,[2] and Saïd Nouira[1]

ABSTRACT.—We studied the reproduction patterns of Squacco Herons, *Ardeola ralloides*, during 2009–2010. This study was carried out in two colonies located at Ichkeul National Park (37.184992 N, 9.633758 E) and Lebna Dam (36.744161 N, 10.916569 E), in northern Tunisia. We determined the reproductive performance of the species, and investigated the relationship between reproductive parameters and nest characteristics (height and diameter). We registered successful nesting, with mean clutch size of 4.51 ± 0.85 for both years combined. Hatching success was 3.67 ± 1.07 eggs hatched/nest and fledging success reached 3.06 ± 1.28 young/nest. All reproductive parameters varied between years. The diameter and the height of nest had no effect on the clutch size, the initial brood size, or the final brood size at each site. We estimated the body condition index (BCI) and the growth curves of developing nestlings from repeated measurements of body mass, tarsus, head and bill length. The last chicks (rank four) to hatch had lower (BCI) and growth rates than the first, the second, and the third hatched chicks. These results stress the need for further protection measures be undertaken at Lebna Dam. Accessibility to the site should be highly controlled by the managers of Tunisian wetlands. *Received 18 August 2013. Accepted 11 January 2014.*

Key words: body condition index, growth rate, Ichkeul, Lebna, reproductive parameters, Squacco Heron.

Squacco Herons, *Ardeola ralloides*, occur in Europe, North West Africa, sub-Saharan Africa and southwest Asia (Hancock and Kushlan 1989, Kushlan and Hafner 2000). In the western Palearctic, nesting sites are widely scattered around the Mediterranean region and in Europe where the species is considered vulnerable. The largest populations occur in eastern Europe where the most serious declines have been reported (Tucker and Heath 1994). In the Mediterranean basin, despite the slight increase of some populations in its western region, the species is rare along the southern shore (Heath and Evans 2000, Kushlan and Hafner 2000). The species' clumped distribution follows the few suitable freshwater areas (Kushlan and Hafner 2000) remaining in a region where losses and deterioration of freshwater feeding and breeding habitat have been recorded (Tucker and Heath 1994, Hafner and Didner 1997).

Squacco Herons typically nest colonially with other species, in small or sometimes large mixed colonies. In the same area, hundreds or thousands of breeding birds coexist including cormorants *Phalacrocorax* spp., Glossy Ibises *Plegadis falcinellus*, and other herons, especially Little Egrets *Egretta garzetta* and Black-crowned Night-Herons *Nycticorax nycticorax*, leading to dense nesting and partitioning in the available space (Jenni 1969, Maxwell and Kale 1977, Parsons 1995).

Generally ardeid species are useful indicators of wetland productivity, trophic structure, human disturbance, and contamination (Custer and Osborn 1977, Dister et al. 1990, Kushlan 1993, Briggs et al. 1998, Osiejuk et al. 1999, Guillemain et al. 2000, Hamel 2011). In fact, any environmental changes which would induce variability in their reproductive parameters are of considerable interest to wildlife and land managers (Temple and Wiens 1989). This is why the breeding biology of colonial herons has been the subject of studies worldwide (Kushlan and Hafner 2000).

Despite the fact that the nesting of birds in Tunisia has been reported by earlier authors (Whitaker 1905, Heim de Balsac and Mayaud 1962, Etchecopar and Hue 1964, Isenmann et al. 2005, Ouni et al. 2009, Ouni et al. 2011), the breeding success of Squacco Herons has not been studied. Though investigations on the breeding success of other species have been already undertaken in Tunisia, such as for Common Blackbirds (*Turdus merula*), Black-shouldered Kites (*Elanus caeruleus*), Laughing Doves (*Spilopelia senegalensis*) and Glossy Ibises (*P. falcinellus*) (Selmi 2004, Ouni 2007, Boukhriss and Selmi 2009, Nefla et al. 2012). Results of these studies stress the need for further surveys considering the importance of wetlands in Tunisia, as Tunisia is known to harbor the most important wetlands in North Africa (e.g., Ichkeul, Sejoumi, Lake of Tunis,

[1] Research Unit "Biodiversity and Population Biology," Department of Biology, University of Sciences of Tunis, El Manar II 2092, Tunis, Tunisia.
[2] Tunisia Wildlife Conservation Society, Bejaoua, Sidi Thebit Tunis, Tunisia.
[3] Corresponding author;
e-mail: aymennefla2007@yahoo.fr

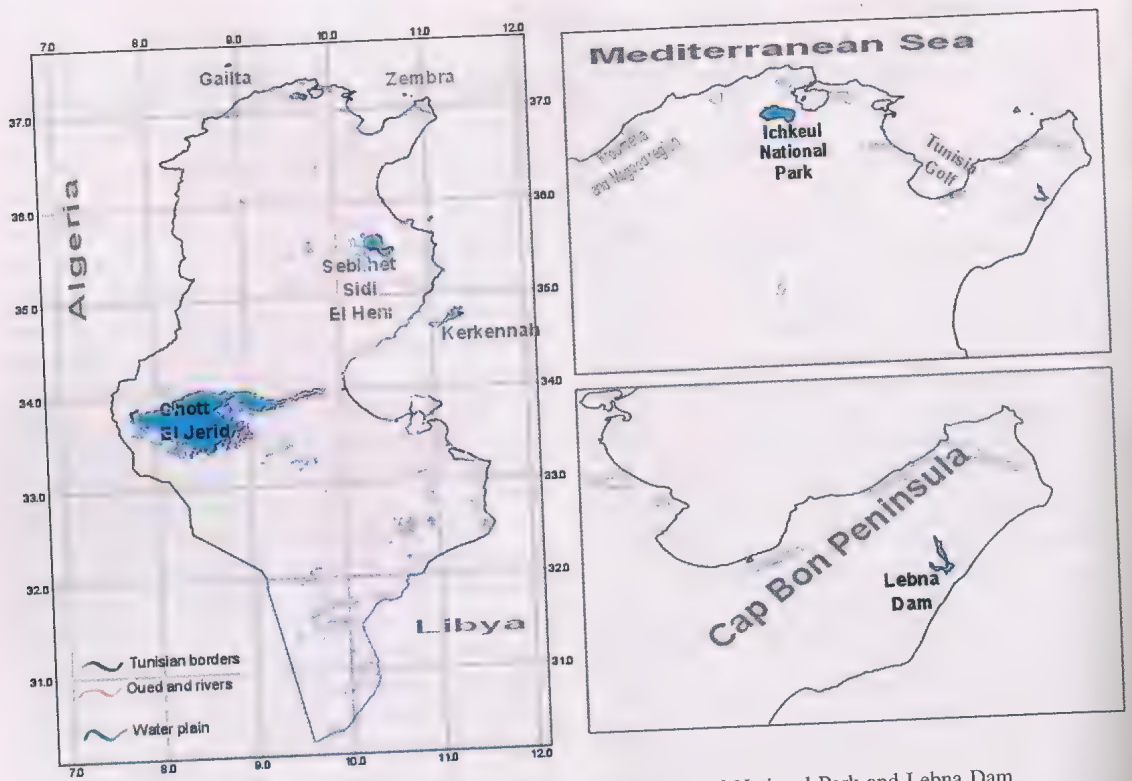


FIG. 1. Map showing location of the nesting areas at Ichkeul National Park and Lebna Dam.

Oued Rmel, Kelbia lagoon). Studies of the breeding success of Squacco Herons in Tunisia seem necessary as there has been limited work related to the species (Hafner 1977, Voisin 1991, González-Martín 1994, Hafner and Didner 1997); only four studies have been carried out regarding the Squacco Heron's reproduction (Sterbetz 1960–1961, Hafner et al. 2001, Delord et al. 2003, Belhadj et al. 2007). Such studies can serve as a basis for studies of the effects of ecological factors on breeding success of the species, particularly predation and competition. Results would help in developing protection programs not only in Tunisian wetlands but across the North African region.

This work aims to describe the breeding biology of Squacco Herons in Tunisia. Our purposes are the evaluation of population size and the description of habitat selection, breeding success, and growth parameters of Squacco Herons in two Tunisian wetlands, the Ichkeul National Park and the Lebna Dam.

METHODS

Study Area.—This study was carried out during 2009–2010 at two sites in northern Tunisia: Ichkeul National Park and Lebna Dam (Fig. 1). Ichkeul National Park (37.184992 N, 9.633758 E) consists of three major habitats: the lagoon (8,500 ha), marshland (2,700 ha), and Ichkeul mountains (1,400 ha). It has been included in the UNESCO list as a Biosphere Reserve (1977) and listed under ''World Heritage Sites'' since 1980. It was considered by the Ramsar Convention (1980) as a Wetland of International Importance. Between 1996–2006, the park has been involved in the list of World Heritage in Danger.

The Lebna Dam is considered one of the most important bird areas in Africa (Fishpool and Evans 2001). It is located in the northeast of Tunisia (36.744161 N, 10.916569 E). It covers a surface of 724 ha. The site is formed by a river and a lagoon. The river pours into the lagoon which drains into the Mediterranean. Lagoon, river banks, and shallow parts provide favorable habitat for the growth of the common reed *Phragmites australis* and the common bulrush *Typha latifolia*. These two plants cover a surface of 40 ha. The flooded zone (20 ha) is covered by herbaceous aquatic plants and the surrounding plains are cultivated by vegetable and cereal crops.

The colony at Ichkeul contained Grey Herons *Ardea cinerea*, Cattle Egrets *Bubulcus ibis*, Little

Egrets *E. garzetta*, Squacco Herons (2009: 60 breeding pairs; 2010: 12 breeding pairs), and Black-crowned Night-Herons *N. nycticorax*. The colony at Lebna contained Glossy Ibises *P. falcinellus* in addition to Cattle Egrets, Little Egrets and Squacco Herons (2009: 25 breeding pairs; 2010: 30 breeding pairs).

Data Collection.—Visits to the study sites were carried out between late April and late July during the two breeding seasons of 2009 and 2010. All nests were constructed in trees (both years). Nest diameter and height (to bottom of structure) and the distance of nests from tree top were measured to the nearest cm for possible association with the birds' reproductive parameters. All sampled nests of Squacco Herons were individually marked with small numbered wooden labels placed below the nest. We studied 43% ($n = 31$) and 80% ($n = 32$) of all constructed nests in Ichkeul and Lebna Dam during both study years, respectively.

Each site was visited weekly (during egg-laying period) and twice (from hatching) to note the number of breeding pairs of each bird species and record nest measurements and positions. Nests were checked with a pole-mounted mirror from the beginning of egg laying. We recorded the number of eggs, hatchlings, and number of chicks surviving per nest until the age of 15 days (when chick scrambling made further visits impractical); that age is our operational criterion for fledging. The clutch was considered complete when there was no change after two consecutive visits.

At the heronry at Ichkeul, a total of 27 nestlings from seven full broods were marked on day 1 for individual recognition and measured every 3 days until day 12. We allocated a size rank for each chick within a brood, according to the tarsus length, measured at the same visit (Thomas et al. 1999); the chick with the longest tarsus was assigned size rank 1, the second longest size was rank 2 and so on. During each visit, we measured tarsus length (from the middle of metatarsal joint to distal end of tarsometatarsus), head length (from the nape to the end of bill), and bill length of each nestling to the nearest 0.1 mm with a vernier caliper. The body mass was measured with a hand-held 500 g Pesola balance.

A body condition index (BCI) was calculated using the residuals of the linear regression equation obtained by correlating the body mass with the tarsus-length (Jakob et al. 1996, Green 2001). The predicted body mass was calculated as equal to a × tarsus length + b where a and b are the slope and intercept parameters, respectively. A positive value for the BCI indicates good body condition.

Data Analyses.—The reproductive parameters were evaluated using: 1) the total mortality rate (number of eggs and young lost/number of eggs laid), 2) the mortality rate of eggs (number of eggs lost/number of eggs laid), 3) the mortality rate of young (number of lost young/number of eggs hatched), 4) the fledging success (number of survivors (final brood size)/number of monitored nest), 5) hatching success (number of eggs hatched (initial brood size)/number of clutches), 6) mean clutch size (number of eggs laid/number of clutches) and 7) breeding success (number of fledglings/number of eggs incubated) (Hafner 1977). The chick/egg ratio was defined as the proportion of eggs hatched in nests where the whole nest did not fail; brood size/clutch size.

Descriptive results are expressed as means and/or percentages in order to facilitate their comparison with results from earlier studies. All statistical analyses were carried out using Statistica 10 software. Data were analyzed using parametric and non-parametric tests. Mean values are given ± SD (standard deviation) and null hypotheses are rejected at $P = 0.05$.

The Mann-Whitney *U*-test was used to compare the height of nest and its distance from tree top. The Student *t*-test was applied to measure the variation of the chicks/eggs ratio between colonies. To compare the reproductive parameters obtained at the two different sites and those recorded in 2009 and 2010 in each one we used the Chi square (X^2) test. Finally, to evaluate the relationship between the reproductive parameters and nest position, the height and the diameter of the nest tree corresponding to each parameter (clutch size, initial brood size and final brood size) were compared using the Kruskall-Wallis test.

RESULTS

Selection of Nesting Sites.—All Squacco Herons built their nests on *Tamarix africana* with a mean height from the ground being 166.5 ± 26.3 cm (range 112–205 cm, $n = 20$). Squacco Herons built their nests on *Acacia horrida* at a mean height of 90.3 ± 40.7 cm (range 42–179 cm, $n = 25$), significantly lower than those at Ichkeul ($Z = 4.85$, $P < 0.001$). In both colonies, nests were built just below the middle of the trees; the mean height of nests was significantly lower (Ichkeul: $Z = -5.41$, $P < 0.001$; Lebna: $Z =$

TABLE 1. Breeding parameters of the Squacco Herons.

Year	Ichkeul			Lebna		
	2009	2010	Combined years	2009	2010	Combined years
Sampled nests	25	6	31	9	23	32
Average clutch size (eggs laid/clutch)	4.56 ± 0.91	4.33 ± 0.51	4.51 ± 0.85	4 ± 1	3.6 ± 0.78	3.71 ± 0.85
Percentage of hatching (%)	80.7	84.6	81.4	63.9	46.9	59.5
Hatching success (eggs hatched/nest)	3.68 ± 1.14	3.66 ± 0.81	3.67 ± 1.07	2.55 ± 1.87	1.69 ± 1.45	1.93 ± 1.6
Percentage of nests with nestlings (%)	96	100	96.8	77.8	60.8	72.7
Percentage of successful nests (%)	92	66.7	87	77.8	47.8	61.35
Mortality (%)	30.7	38.5	32.15	47.2	66.3	56.3
Fledging success (survivors/nest)	3.16 ± 1.21	2.66 ± 1.63	3.06 ± 1.28	2.11 ± 1.69	1.21 ± 1.34	1.46 ± 1.48
Breeding success (%)	69	61	67	52	33	43

-6.06, $P < 0.001$) than the mean distance of nests from the tree top (Ichkeul: 491 ± 106 cm, $n = 20$; Lebna: 355.3 ± 32.3 cm, $n = 25$).

Reproductive Performance.—The overall mean clutch size (both sites) was 4.11 ± 0.93 eggs per nest ($n = 63$), with clutches of four (41.3% of total clutches), five (30.1%), three (19%), two (4.8%) and six eggs (4.8%). The chick/egg ratio varied between colonies ($t = -3.5$, df = 61, $P < 0.001$) and was 0.52 (Lebna) and 0.82 (Ichkeul). Likewise, clutch size ($X^2 = 34.32$, df = 2, $P < 0.001$), hatching success ($X^2 = 25.31$, df = 2, $P < 0.001$) and fledging success ($X^2 = 17.43$, df = 2, $P < 0.01$) varied between colonies. All reproductive parameters of Squacco Herons recorded at Lebna were significantly lower than at Ichkeul (Table 1). The total mortality measured at Lebna during both phases (incubation and 2 weeks rearing) was significantly higher than that recorded at Ichkeul. Squacco Herons lost respectively in Ichkeul and Lebna, 18.6% and 47.9% of their eggs during the first phase and 16.7% and 26.3% of their young in the second.

All reproductive parameters slightly varied between years within Ichkeul (clutch size ($X^2 = 16$, df = 3, $P < 0.01$), hatching success ($X^2 = 15.58$, df = 4, $P < 0.01$), and fledging success ($X^2 = 16.62$, df = 4, $P < 0.01$)). We recorded the highest clutch size (six eggs) and brood size (five chicks) (Table 2). At Lebna, the clutch size ($X^2 = 53.33$, df = 3, $P < 0.001$), the hatching success ($X^2 = 100.83$, df = 5, $P < 0.001$) and the fledging success ($X^2 = 96$, df = 4, $P < 0.001$) varied between years. In both sites, reproductive parameters reached their maximum in 2009 (Table 1).

Relationship between Reproductive Parameters and Nest Position.—The height of the nest had no effect on the reproductive parameters of the species at Ichkeul (clutch size (H (2, $n = 20$) = 4.26, $P = 0.11$), the initial brood size (H (2, $n = 20$) = 2.06, $P = 0.35$) and the final brood size (H (2, $n = 20$) = 0.45, $P = 0.79$)) and Lebna (clutch size (H (2, $n = 25$) = 1.7, $P = 0.42$), the initial brood size (H (2, $n = 25$) = 1.69, $P = 0.42$) and the final brood size (H (2, $n = 25$) = 2.74, $P = 0.25$)). We found no relation between the diameter of nest and reproductive parameters at Ichkeul (clutch size (H (2, $n = 20$) = 1.48, $P = 0.47$), the initial brood size (H (2, $n = 20$) = 2.53, $P = 0.28$), and the final brood size (H (2, $n = 20$) = 3.04, $P = 0.21$)) and Lebna (clutch size (H (2, $n = 25$) = 2.14, $P = 0.34$), the initial brood size (H (2, $n = 25$) = 4.24, $P = 0.11$), and the final brood size (H (2, $n = 25$) = 3.14, $P = 0.2$)).

Growth Rates and Body Condition Index of Chicks.—Growth rates for the four variables were linear for the age interval (1–12 days) considered (Table 3). Tarsus-length and body mass were positively and linearly ($R = 0.96$, $P < 0.001$, $n = 27$) related. We calculated a body condition index BCI, including all the chicks measured, as: BCI = Observed body mass − ($-35.61 + 3.76 \times$ observed tarsus-length). Our results indicate variations in the BCI of the chicks with chick size rank. Rank four chicks had the lowest BCI (-4.76 ± 1.52) compared to rank one (0.89 ± 4.41), rank two (2.5 ± 0.65) and rank three (2.25 ± 2.28). Equally,

TABLE 2. Clutch and brood size.

Sites		Ichkeul						Lebna					
		2009		2010		Combined years		2009		2010		Combined years	
Year	*n* (clutch)	25%		6%		31%		9%		23%		32%	
Eggs per nest	2	0	-	0	-	0	-	1	11.1	2	8.7	3	9.4
	3	4	16	0	-	4	13	1	11.1	7	30.4	8	25
	4	6	24	4	66.7	10	32.3	4	44.4	12	52.2	16	50
	5	12	48	2	33.3	14	45.2	3	33.3	2	8.7	5	15.6
	6	3	12	0	-	3	9.5	0	-	0	-	0	-
Young per nest	0	2	8	1	16.7	3	9.5	2	22.2	12	52.2	14	43.7
	1	0	-	0	-	0	-	2	22.2	0	-	2	6.2
	2	2	8	2	33.3	4	13	1	11.1	5	21.7	6	18.8
	3	11	44	0	-	11	35.5	1	11.1	6	26.1	7	21.9
	4	8	32	3	50	11	35.5	3	33.3	0	-	3	9.4
	5	2	8	0	-	2	6.5	0	-	0	-	0	-

differential growth was associated with hatch rank. The last hatchling had the lowest growth rate for all variables compared to others hatchlings ranks.

DISCUSSION

Reproductive parameters of birds may present temporal and spatial variations (Ogden et al. 1980, Rotenberry and Wiens 1989, Jarvinen 1993, Saether et al. 1999, Dreitz et al. 2001). The clutch size is often dependent on the territory quality (Hogstedt 1980) and the age of the parents (younger parents laying smaller number of eggs (Coulson 1966, Klomp 1970, Coulson and Porter 1985)). In the case of herons, despite the fact that temporal variation of the clutch size has been reported (Custer et al. 1983), Tremblay and Ellison (1980) recorded the same clutch size between years. Data reported herein show that the reproductive parameters of Squacco Herons varied significantly between areas and years.

Considering Ichkeul National Park, clutch size, hatching success and fledging success were similar to those recorded on the northern shore of the Mediterranean basin; they were larger than those measured at the Tonga Lake (a north African site) (Belhadj et al. 2007). Lebna Dam showed lower reproductive parameter values compared

TABLE 3. Growth rates of Squacco Heron chicks from 1–12 days of age.

	Hatching order	Mean	Intercept	r^2	*P*	*n* (chicks)
Mass gain (g/d)	A	10.12	−8.33	0.98	0.009	7
	B	11.11	−16.26	0.95	0.02	7
	C	10.52	−21.33	0.93	0.03	7
	D	3.53	−0.25	0.92	0.03	6
	all chicks	8.6	−8.52	0.95	0.02	27
Tarsus growth (mm/d)	A	2.96	5.31	0.99	0.005	7
	B	2.9	5.21	0.97	0.01	7
	C	2.62	4.44	0.95	0.02	7
	D	1.62	5.38	0.95	0.02	6
	all chicks	2.45	6.05	0.96	0.01	27
Head growth (mm/d)	A	4.2	15	0.98	0.007	7
	B	4.23	14.14	0.99	0.005	7
	C	4.02	12.11	0.95	0.02	7
	D	2.77	13.92	0.93	0.03	6
	all chicks	3.38	17.98	0.93	0.03	27
Beak growth (mm/d)	A	2.01	7	0.99	0.003	7
	B	1.99	6.54	0.98	0.007	7
	C	2.19	3.96	0.97	0.01	7
	D	1.51	4.43	0.96	0.01	6
	all chicks	1.87	6.20	0.97	0.01	27

TABLE 4. Clutch size, hutching success, and fledging success of Squacco Herons from previous studies and this study.

Region	Mean clutch size	Hutching success	Fledging success	Source
Camargue (France)	4.7 ± 0.7	–	–	Hafner 1977
Eastern Europe	4.6 ± 1.1	–	–	Sterbetz 1960–1961
Ichkeul	4.51 ± 0.85	3.67 ± 1.07	3.06 ± 1.28	present study
Rhône Delta (France)	4 ± 1.05	2.4 ± 1.28	1.8 ± 0.02	Delord et al. 2003
Tonga Lake (Algeria)	3.73 ± 0.7	3.2 ± 0.67	2.8 ± 0.67	Belhadj et al. 2007
Lebna	3.71 ± 0.85	1.93 ± 1.6	1.46 ± 1.48	present study

with those of sites in Ichkeul and Europe (Hafner 1977, Sterbetz 1960–1961, Delord et al. 2003) (Table 4). These values are in fact similar to those reported for the north African site (Belhadj et al. 2007).

The observed spatial variation is to be expected knowing the conservation statutes of the sites. In Ichkeul National Park conservation plans are being applied; several reports followed the conservation of the park's fauna and flora from 2003–2009 (Chauvelon et al. 2003; ANPE 2004, 2005, 2006, 2007, 2008, 2009). The heronry of Ichkeul is located at the mouth of Oued Sejnene which is a flooded zone. These criteria made the site naturally more protected against terrestrial predators than Lebna Dam. Lebna Dam is not covered by any conservation plans despite the fact it is an African Important Bird Area (Fishpool and Evans 2001).

In periods of low precipitation, a clear lowering of the water level creates a path for terrestrial predators (both human [egg theft] and others) and causes loss of eggs and chicks (Nefla et al. 2012). This phenomenon affects the reproductive parameters of breeding birds and reduces hatching and fledging success of Squacco Herons and other neighboring herons (Little Egrets and Cattle Egrets) (AN, pers. obs.). It is known that in mixed-species heronries, nest characteristics are known to influence reproductive success of birds (Coulson 1968, Hafner 1977, Buckley and Buckley 1980, Burger and Gochfeld 1988, Bosch and Sol 1998, Larison et al. 2001). Burger (1982) noted that the advantage of nesting high in trees may relate to increased visibility of predators, increased ability to make quick flight when predators approach and decreasing losses to ground predators. Fasola and Alieri (1992) reported other benefits resulting from the height of the nest. They indicated that larger herons nest at higher elevations, because movement is easier among the tall and open branches, while the smaller herons prefer lower elevations, because they attain greater protection from aerial predators. These results are not concordant with ours revealed in Lebna Dam. The high mortality affected mainly nests of Squacco Herons (smallest species) who built their nests at the lowest level (88 ± 34.99 cm) compared to other neighboring herons. However, in accordance with this study, other authors have demonstrated the absence of a relationship between nest heights or diameters and the reproductive parameters of egrets (Ferguson 1994, Kazantzidis et al. 1997, Si Bachir et al. 2000, Parejo et al. 2001).

The growth curve of very young (up to day 12) Squacco Heron nestlings at Ichkeul is marginally similar to that found for Cattle Egrets and the Purple Herons in northeastern Algeria (Samraoui et al. 2007, Nedjah et al. 2010). In accordance with the universal pattern for all herons studied, a differential growth of Squacco Heron chicks was associated with hatch rank. The last hatchling had the lowest growth rate compared to other hatchlings' ranks. In Ichkeul, we found that the last chick had the lowest BCI; this is in accordance with results of Delord et al. (2003) in the Rhône Delta. The variation of the BCI related to the rank of chick size may indicate that competition between siblings resulted in different quantities of food eaten by the older and larger chicks. This agrees with the idea that the observed reduction of the brood in many species of herons is because of food shortage (Lack 1949, Mock and Parker 1986).

This work provides evidence for the need to conduct monitoring programs, aiming toward the conservation of biodiversity, including for the Squacco Herons, at Lebna Dam. Several monitoring programs at Ichkeul National Park have been conducted in association with conservation of biodiversity and management of protected areas plans. These programs focus on management of protected areas, diagnosis, and establishment of guidelines for the planning and directing of Action Plans, most of which cover a 5-year period (DCNMR 2002). The authors are keen to develop a more sustainable development

program of Lebna Dam focusing on environmental resources but taking into account cultural dimensions of the region.

ACKNOWLEDGMENTS

We thank the Ministry of Agriculture of Tunisia, General directorate of forests and the curator of Ichkeul National Park, who authorized access to the site. We also express our gratitude to members of the research unit "Biodiversity and Population Biology", Faculty of Sciences of Tunis.

LITERATURE CITED

Agence Nationale de Protection de l'Environnement (Anpe). 2004. Le suivi scientifique au Parc National de l'Ichkeul. Ministère de l'Agriculture, de l'Environnement et des Ressources Hydrauliques, Agence Nationale de Protection de l'Environnement, Tunisia.

Agence Nationale de Protection de l'Environnement (Anpe). 2005. Le suivi scientifique au Parc National de l'Ichkeul. Ministère de l'Agriculture, de l'Environnement et des Ressources Hydrauliques, Agence Nationale de Protection de l'Environnement, Tunisia.

Agence Nationale de Protection de l'Environnement (Anpe). 2006. Le suivi scientifique au Parc National de l'Ichkeul. Ministère de l'Agriculture, de l'Environnement et des Ressources Hydrauliques, Agence Nationale de Protection de l'Environnement, Tunisia.

Agence Nationale de Protection de l'Environnement (Anpe). 2007. Le suivi scientifique au Parc National de l'Ichkeul. Ministère de l'Agriculture, de l'Environnement et des Ressources Hydrauliques, Agence Nationale de Protection de l'Environnement, Tunisia.

Agence Nationale de Protection de l'Environnement (Anpe). 2008. Le suivi scientifique au Parc National de l'Ichkeul. Ministère de l'Agriculture, de l'Environnement et des Ressources Hydrauliques, Agence Nationale de Protection de l'Environnement, Tunisia.

Agence Nationale de Protection de l'Environnement (Anpe). 2009. Le suivi scientifique au Parc National de l'Ichkeul. Ministère de l'Agriculture, de l'Environnement et des Ressources Hydrauliques, Agence Nationale de Protection de l'Environnement, Tunisia.

Belhadj, G., Y. Chabi, B. Chalabi, and M. Gauthier-Clerc. 2007. The breeding biology of the Cattle Egret *Ardea ibis*, the Little Egret *Egretta garzetta*, the Squacco Heron *Ardeola ralloides*, the Black-Crowned Night Heron *Nycticorax nycticorax*, the Purple Heron *Ardea purpurea* and the Glossy Ibis *Plegadis falcinellus*, at the Lake Tonga, Algeria. European Journal of Scientific Research 19:58–78.

Bosch, M. and D. Sol. 1998. Habitat selection and breeding success in Yellow-legged Gulls *Larus cachinnans*. Ibis 140:415–421.

Boukhriss, J. and S. Selmi. 2009. Nidification et succès reproducteur de la tourterelle maillé *Streptopelia senegalensis* dans une oasis du sud tunisien. Alauda 77:187–192.

Briggs, S. V., W. G. Lawler, and S. A. Thornton. 1998. Relationships between control of water regimes in River Red Gum wetlands and abundance of water birds. Corella 22:47–55.

Buckley, F. G. and P. A. Buckley. 1980. Habitat selection and marine birds. Pages 69–112 *in* Behavior of marine animals. Volume 6. Marine birds (J. Burger, B. L. Olla and H. E. Winn, Editors). Plenum Press, New York, USA.

Burger, J. 1982. On the nesting location of Cattle Egrets *Bubulcus ibis* in South African heronries. Ibis 124:523–529.

Burger, J. and M. Gochfeld. 1988. Nest site selection by Laughing Gull: comparison of tropical colonies (Culebra, Puerto Rico) with temperate colonies (New Jersey). Condor 87:364–373.

Chauvelon, P., A. Mauchamp, M. Smart, and P. Tomas-Vives. 2003. Programme de suivi du Parc National de l'Ichkeul (Tunisie). Ministère de l'Agriculture, de l'Environnement et des Ressources en Eau, Agence Nationale de Protection de l'Environnement, Tunisia.

Coulson, J. C. 1966. The influence of the pair bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. Journal of Animal Ecology 35:269–279.

Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217:478–479.

Coulson, J. C. and J. M. Porter. 1985. Reproductive success of the Kittiwake Gull *Rissa tridactyla*: the role of clutch size, chick growth rates and parental quality. Ibis 127:450–466.

Custer, T. W. and R. G. Osborn. 1977. Wading birds as biological indicators: 1975 colony survey. United States Department of the Interior, Fish and Wildlife Service, Special Scientific Report Wildlife No 206, USA.

Custer, T. W., G. L. Hensley, and T. E. Kaier. 1983. Clutch size, reproductive success, and organochlorine contaminants in Atlantic coast Black-crowned Night-Herons. Auk 100:699–710.

Delord, K., Y. Kayser, C. Barbraud, and H. Hafner. 2003. Variability in breeding parameters of the Squacco Heron *Ardeola ralloides*. Bird Study 50:300–305.

Direction de la Conservation de la Nature et du Milieu Rural (DCNMR). 2002. Gestion des aires protégées Diagnostic, orientations d'aménagement et de gestion Plan d'Actions sur 5 ans. Ministère de l'environnement et de l'aménagement du territoire, Direction Générale de l'Environnement et de la Qualité de la Vie. Tunisia.

Dister, E, D. Gomer, P. Obrdlik, P. Petermann, and E. Schneider. 1990. Water Management and ecological perspectives of the Upper Rhine's floodplains. River Research and Applications 5:1–15.

Dreitz, V. J., R. E. Bennetts, B. Toland, W. M. Kitchens, and M. W. Collopy. 2001. Spatial and temporal variability in nest success of Snail Kites in Florida: a meta-analysis. Condor 113:502–509.

Etchecopar, R. D. and F. Hue. 1964. Les Oiseaux du Nord de l'Afrique. Boubée N et Cie. Paris, France.

Fasola, M. and R. Alieri. 1992. Nest site characteristics in relation to body size in herons in Italy. Colonial Waterbirds 15:185–192.

FERGUSON, J. W. H. 1994. Do nest site characteristics affect the breeding success of Red Bishops *Euplectes orix*? Ostrich 65:274–280.

FISHPOOL, L. D. C. AND M. I. EVANS. 2001. Important Bird Areas in Africa and associated islands: priority sites for conservation. Newbury and Cambridge, Pisces Publications and BirdLife International, UK.

GONZÁLEZ-MARTÍN, M. 1994. Reproduccion de la garza imperial (Ardea purpurea) en el delta del Ebro. Thesis. University of Barcelona, Spain.

GREEN, A. J. 2001. Mass/tarsus-length residuals: measures of body condition or generators of spurious results. Ecology 82:1473–1483.

GUILLEMAIN, M., S. HOUTE, AND H. FRITZ. 2000. Activities and food resources of wintering teal (*Anas crecca*) in a diurnal feeding site: a case study in western France. Revue d'Ecologie Terre et Vie 55:171–181.

HAFNER, H. 1977. Contribution à l'étude de quatre espèces de hérons (*Egretta garzetta* L., *Ardeola ralloides* Scop., *Ardeola ibis* L., *Nycticorax nycticorax* L.) pendant leur nidification en Camargue. Thesis. Université Paul Sabatier de Toulouse, France.

HAFNER, H. AND E. DIDNER. 1997. Species account on the Squacco Heron *Ardeola ralloides*. Birds of the Western Palearctic Update 1:166–174.

HAFNER, H., R. E. BENNETTS, AND Y. KAYSER. 2001. Changes in clutch size, brood size and numbers of nesting Squacco Herons (*Ardeola ralloides*) over a 32-year period in the Camargue, South France. Ibis 143:11–16.

HAMEL, J. 2011. Utilisation des oiseaux aquatiques comme bioindicateurs de l'intégrité des lacs de montagne marocains. Dissertation. Université de Sherbrooke, Québec, Canada.

HANCOCK, J. AND J. A. KUSHLAN. 1989. Guide des hérons du monde – aigrettes – bihoreaux – butors – hérons – onorés. Delachaux & Niestlé, Paris, France.

HEATH, M. F. AND M. I. EVANS. 2000. Important Bird Areas in Europe. BirdLife International. Cambridge, UK.

HEIM DE BALZAC, H. AND N. MAYAUD. 1962. Les Oiseaux du Nord-Ouest de l'Afrique. Paul Chevalier, Paris, France.

HOGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210:1148–1150.

ISENMANN, P., T. GAULTIER, A. EL HILI, H. AZAFZAF, H. DLENSI, AND M. SMART. 2005. Les Oiseaux de la Tunisie - Birds of Tunisia. Société d'Etudes Ornithologiques de France, Muséum National d'Histoire Naturelle, Paris, France.

JAKOB, E. M., S. D. MARSHALL, AND G. W. UETZ. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

JARVINEN, A. 1993. Spatial and temporal variation in reproductive traits of adjacent northern Pied Flycatcher *Ficedula hypoleuca* populations. Ornis Scandinavica 2:33–40.

JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. Ecological Monographs 39:243–270.

KAZANTZIDIS, S., V. GOUTNER, M. PYROVETSI, AND A. SINIS. 1997. Comparative nest site selection and breeding success in 2 sympatric ardeids, Black-crowned Night-Heron *Nycticorax nycticorax* and Little Egret *Egretta garzetta* in the Axios Delta, Macedonia, Greece. Colonial Waterbirds 20:505–517.

KLOMP, H. 1970. The determinants of clutch size in birds. Ardea 58:1–54.

KUSHLAN, J. A. 1993. Colonial waterbirds as bioindicators of environmental change. Colonial Waterbirds 16: 223–251.

KUSHLAN, J. A. AND H. HAFNER. 2000. Heron conservation. Academic Press, London, UK.

LACK, D. 1949. Family size in certain thrushes. Evolution 3:57–66.

LARISON, B., S. A. LAYMON, P. L. WILLIAMS, AND T. B. SMITH. 2001. Avian responses to restoration: nest site selection and reproductive success in Song Sparrow. Auk 118:432–442.

MAXWELL, G. R. AND H. W. KALE. 1977. Breeding biology of five species of herons in coastal Florida. Auk 94:689–700.

MOCK, D. W. AND G. A. PARKER. 1986. Advantages and disadvantages of egret and heron brood reduction. Evolution 40:459–470.

NEDJAH, R., A. BOUCHEKER, F. SAMRAOUI, R. MENAI, A. ALFARHAN, K. A. S. AL-RASHEID, AND B SAMRAOUI. 2010. Breeding ecology of the Purple Heron *Ardea purpurea* in Numidia, north-eastern Algeria. Ostrich 81:189–196.

NEFLA, A., R. OUNI, AND S. NOUIRA. 2012. The breeding status of the Glossy Ibis *Plegadis falcinellus* in the Lebna Dam in Cap Bon, Tunisia. Journal of Life Sciences 6:776–782.

OGDEN, J. C., H. W. KALE, AND S. A. NESBITT. 1980. The influence of annual variation in rainfall and water levels on nesting by Florida populations of wading birds. Transactions of the Linnean Society of New York 9:115–126.

OSIEJUK, T. S., L. KUCZYNSKI, AND A. JERMACZEK. 1999. The effects of water conditions on breeding communities of pastures, meadows and shrub habitats in the Slonsk reserve, N-W Poland. Biologia 54:207–214.

OUNI, R. 2007. Distribution et reproduction de l'elanion blanc (*Elanus caeruleus*) en Tunisie. Ostrich 78:395–399.

OUNI, R, A. NEFLA, AND A. EL HILI. 2009. Nidification de l'Ibis falcinelle *Plegadis falcinellus* au Cap Bon (Tunisie). Alauda 77:115–120.

OUNI, R, A. NEFLA, A. EL HILI, AND S. NOUIRA. 2011. Les populations d'ardéidés nicheurs en Tunisie. Alauda 79:157–166.

PAREJO, D., J. M. SANCHEZ, AND J. M. AVILES. 2001. Breeding biology of the Cattle Egret *Bubulcus ibis* in south-west Spain. Bird Study 48:367–372.

PARSONS, K. C. 1995. Heron nesting at Pea Patch Island, Upper Delaware Bay, USA: abundance and reproductive success. Colonial Waterbirds 18:69–78.

ROTENBERRY, J. T. AND J. A. WIENS. 1989. Reproductive Biology of shrub steppe passerine birds: geographical

and temporal variation in clutch size, brood size, and fledging success. Condor 91:1–14.

SÆTHER, B. E., T. H. RINGSBY, Ø. BAKKE, AND E. J. SOLBERG. 1999. Spatial and temporal variation in demography of a House Sparrow meta-population. Journal of Animal Ecology 68:628–637.

SAMRAOUI, F., R. MENAI, AND B. SAMRAOUI. 2007. Reproductive ecology of the Cattle Egret (*Bubulcus ibis*) at Sidi Achour, north-eastern Algeria. Ostrich 78:481–487.

SELMI, S. 2004. Nidification et succès reproducteur du Merle noir *Turdus merula* dans les oasis du sud Tunisien. Alauda 72:23–31.

SI BACHIR, A., H. HAFNER, J. N. TOURENQ, AND S. DOUMANDJI. 2000. Structure de l'habitat et biologie de reproduction du Héron Garde-bœuf, *Bubulcus ibis*, dans une colonie de la vallée de la Soummam (Petite Kabylie, Algérie). Revue d'Ecologie (Terre et Vie) 55:33–43.

STERBETZ, I. 1960–1961. The Squacco Heron in the Sasér bird sanctuary. Aquila 67–68:39–70.

TEMPLE, S. A. AND J. A. WIENS. 1989. Bird populations and environment changes: can birds be bioindicators? American Birds 43:260–270.

THOMAS, F., Y. KAYSER, AND H. HAFNER. 1999. Nestling size rank in the Little Egret (*Egretta garzetta*) influences subsequent breeding success of offspring. Behavioral Ecology and Sociobiology 45:466–470.

TREMBLAY, J. AND L. N. ELLISON. 1980. Breeding success of the Black-crowned Night-Heron in the St. Lawrence estuary. Canadian *Journal* of Zoology 58: 1259–1263.

TUCKER, G. M. AND M. F. HEATH. 1994. Birds in Europe: their conservation status. BirdLife International. Cambridge, UK.

VOISIN, C. 1991. The herons of Europe. T. & A.D. Poyser, London, UK.

WHITAKER, J. I. S. 1905. The birds of Tunisia. Volume 2. R. H. Porter, London, UK.

The Wilson Journal of Ornithology 126(2):401–405, 2014

Locating Alexander Wilson's Bristol Township and the Milestown School

Albert Filemyr[1] and Jeff Holt[2,3]

ABSTRACT.—The correction of a long standing error in what was thought to be the location of the Milestown School where Alexander Wilson, the Father of American Ornithology, taught from 1796 to 1801. *Received 21 October 2013. Accepted 11 February 2014.*

Key words: Alexander Wilson, Bristol Township, Milestown, Milestown School, Wilson.

Two years after his arrival in the New World, Alexander Wilson- not yet "The Father of American Ornithology" - accepted a position as teacher at the Milestown School in Pennsylvania. Five years later, in 1801, Wilson moved to Bloomfield, New Jersey, where he briefly taught before assuming a new position at the Union School at Gray's Ferry, Philadelphia, in February 1802. The history and circumstances of the schools in Bloomfield and Gray's Ferry are well known, but the location of the Milestown School has consistently been misidentified in the literature treating Wilson's biography and movements in America.

In a recently published biography, *Alexander Wilson: The Scot Who Founded American Ornithology*, the authors, Edward H. Burtt, Jr. and William E. Davis, Jr., write: "……..in 1796, settled about 20 miles northwest of Philadelphia in Milestown where he taught school until July 1801." (Burtt and Davis 2013:27). The source of the statement in the Burtt/Davis book may have come from two previously published books on Wilson. In the 1961 book written by Robert Cantwell titled *Alexander Wilson: Naturalist and Pioneer, A Biography*, he wrote that "Milestown was within the limits of Bristol Township, nineteen miles from the center of Philadelphia. The Old York Road, to Trenton and on to New York, ran through Bristol, which stood on the Delaware River;…Just inside the Bristol limits was Barkham's Lane, and Wilson's schoolyard beyond it." (Cantwell 1961:89). Thereafter, Clark Hunter in his 1983 book, *The Life and Letters of Alexander Wilson*, wrote the "school at Milestown, some 20 miles from Philadelphia, more or less on the road to Trenton and New York" (Hunter 1983:65). Based on these references, our initial search for the school in Milestown started in Bristol Township, Bucks County, Pennsylvania which is along the

[1] 1314 Lenore Road, Meadowbrook, PA 19046, USA.
[2] 1215 Taft Avenue, Woodbury, NJ 08096, USA.
[3] Corresponding author; e-mail: jefflaw@msn.com

FIG. 1. This detail from the 1808 map by John Hills (surveyed 1801–1807) titled ''Plan of the City of Philadelphia and Environs'' clearly shows Bristol Township located in Philadelphia County. This area is now within the present day boundary of the City of Philadelphia. (From the collection of the American Philosophical Society, Philadelphia PA. Used with permission. Hills 1808).

Delaware River about 18 miles from Center City Philadelphia. Research into the history of this Bristol Township failed to uncover any mention of a Milestown or a school associated with that town. This was our first indication that Cantwell and others may have gotten the location of Milestown wrong.

Additional comments made by Cantwell also suggest that the search might need to begin elsewhere. Cantwell notes that during his tenure at Milestown, Wilson bought a horse and ''began making trips into Bucks County north of Milestown'' (Cantwell 1961:100). While not dispositive, this statement nevertheless suggested that if Milestown was actually located in today's Bristol Township, then Wilson was already living in Bucks County and thus, would not be making trips **into** Bucks County.

Further evidence to suggest that the location of Milestown is not in Bristol Township, Bucks County can be found in a letter dated August 22, 1798 from Wilson to his father in Scotland and reprinted in volume one of the 1876 two volume set of books titled *The Poems and Literary Prose of Alexander Wilson.* In that letter, Wilson indicates that the letter was written from ''Milestown, Bristol Township, Philadelphia County'' (Grosart 1876:63). Certainly, Wilson himself must have known where he was living. Thus three questions. Was there a Bristol Township located within the geographic boundary of Philadelphia County? If so, was there a Milestown in that Bristol Township? And further, was there a school in that community? The answers to these three questions are yes. There was a Bristol Township within Philadelphia County (Fig. 1), there was a Milestown in that township (Fig. 3), and there was a school in Milestown (Fig. 2). In fact there is still a school on the general site of the Milestown School. (Fig. 3)

Milestown (or Miles Town) can date its history to 1695 when Griffith Miles acquired 250 acres of

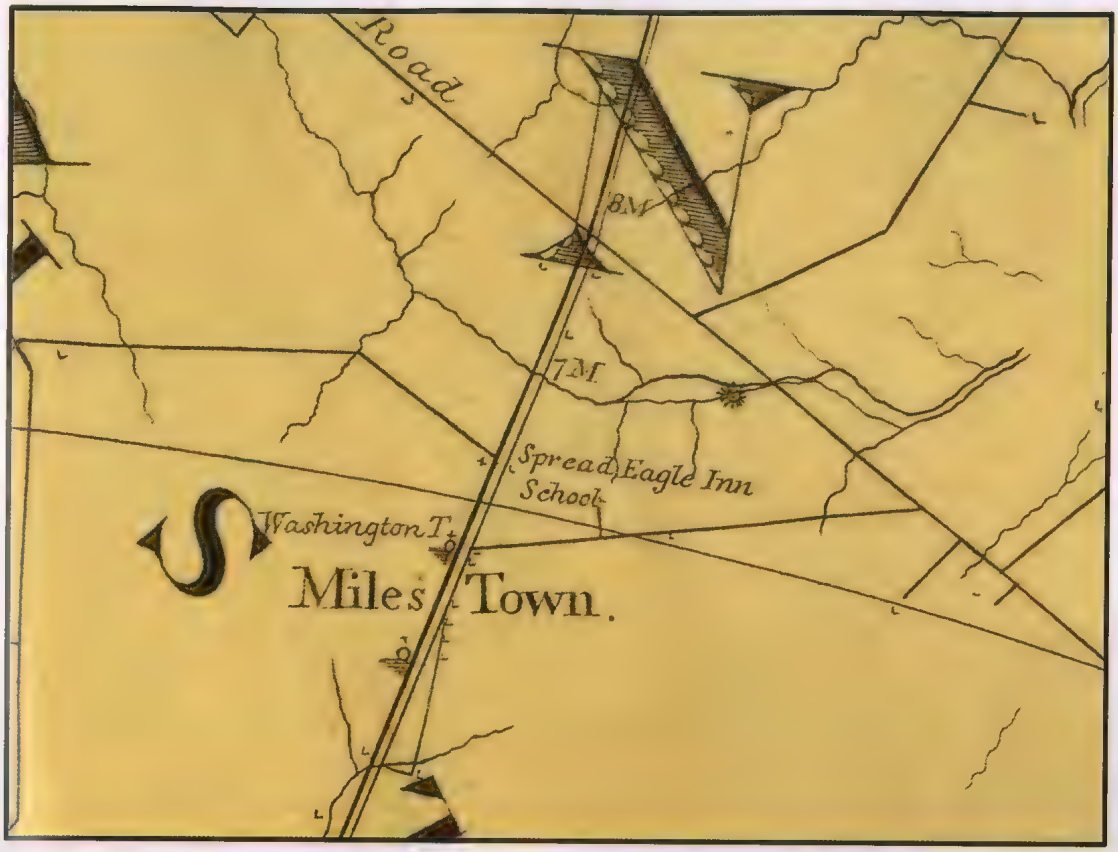


FIG. 2. This detail from the 1808 John Hills map (surveyed 1801–1807) titled "Plan of the City of Philadelphia and Environs" clearly shows Milestown located within Bristol Township, Philadelphia County. It also shows the location of the Spread Eagle Inn and the Milestown School. (From the collection of the American Philosophical Society, Philadelphia PA. Used with permission. Hills 1808).

land and built a cabin where the intersection of Haines Street and Old York Road now exists in the Oak Lane section of Philadelphia (Mears 1890). This is 7.5 miles north of center city Philadelphia (Fig. 4). Shortly thereafter, other Welsh families settled in the area and it became known as Milestown. This geographic area of Philadelphia County was then known as Bristol Township (Fig. 1).

In 1745, a one-story school house was built in Milestown. The authors, and previous researchers, have been unable to locate any records of this school prior to 1761. In 1761, Joseph Armitage, who owned the school building and the land it was on, gave the building and a quarter acre of land, located within "one square of York Road" to a group of citizens to act as trustees of the land and the school (Mears 1890:52). The school was called the Milestown (and occasionally Armitage) School (Fig. 2).

In 1791, trustees of the school agreed that the school house could also be used as a house of worship. Two local congregations shared space in alternating Sunday afternoons. This decision is of interest to students of ornithology as John Bachman, while studying for the ministry, taught at the Milestown School a few years after Wilson. In the early 1870s, the then Reverend Bachman, who had collaborated with John James Audubon in the production of *The Viviparous Quadrupeds of North America* (and whose daughters married Audubon's sons), wrote regarding his time at Milestown: "I have some pleasant reminiscences of the old school house at Milestown. It was there that Wilson, the ornithologist, first tried his hand as a pedagogue... Wilson visited us occasionally from Philadelphia and I always joined him on Saturdays in looking for specimens in ornithology." (Mears 1890:56)

In a four page history of the Milestown School, authored in 1884 and located in the Account Book

FIG. 3. This present day map of the area in Philadelphia once known as Milestown shows Pennsylvania Route 611 (Old York Road), North Broad Street, Oak Lane Avenue and the Ellwood School. (© OpenStreetMap contributors, DeBrandt 2013; www.opendatacommons.org/licenses/odbl.deBrandt).

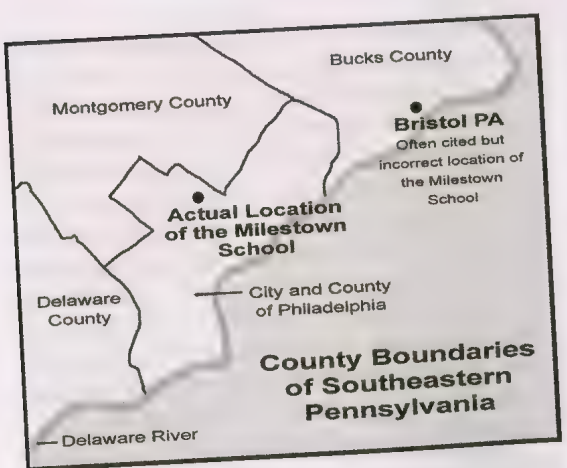


FIG. 4. Counties of southeastern Pennsylvania showing the actual location of the Milestown being in the present City and County of Philadelphia as opposed to the often cited but incorrect location in Bristol, Bucks County.

of The Trustees of the Milestown School, 1797–1884 among the early teachers noted are:

"Alexander Wilson, the Ornithologist"

"John Bachman, a student of divinity….who later was a pastor of St. John's Lutheran Church in Charlestown, SC." (Account Book 1884: unnumbered)

The school house where both Wilson and Bachman taught was replaced in 1818 on the same general site. This new school, known as the Octagonal School, lasted until 1875 when it was transferred to the School District of Philadelphia (Mears 1890). It had been in private control since 1745. By this time it was known as the Ellwood School. A new building was erected in 1875 and lasted until 1957 when the current Ellwood School was built (Ellwood 1950). All the previous buildings, and the current building, were and are on the same general site first used in 1745. The current address for the Ellwood School is 6701 N 13th St, Philadelphia, PA 19126 (Fig. 3).

Additional support for the location of the Milestown School being in Philadelphia County can be found in multiple comments contained in the letters of both Wilson and Bachman who mention that during their respective tenures at Milestown, they lived at a boarding house operated by the Kulps (Grosart 1876, Mears 1890). United States Censuses from this time identify two Kulps (Isaac Kulp and Isaac Kulp, Jr.) having residences in Bristol Township, Philadelphia County (1790 US Census, 1800 US Census). In 1724, Benjamin Armitage built a public house on York Road, across from Haines Street. This property was bought by Jacob Kulp in 1790 and sold to his son, Isaac, in 1797, who operated the Inn until 1810 (Mears 1890). The 1808 map of Milestown identifies a "Spread Eagle Inn" on York Road (Fig 2), across from what is now Haines Street. Bachman in one of his letters further notes that the Kulp boarding house was located "a few hundred yards" from the Milestown school house (Mears 1890:56). This distance matches approximately the site of the school and the York Road/Haines Street intersection.

So how did Cantwell (and others) mislocate Milestown and the school? The answer lies in the evolution of the city of Philadelphia and of Philadelphia County. Originally, the city of Philadelphia was confined generally to the area now known as Center City. Philadelphia County extended well beyond the city limits. As the population grew, the county areas outside the city borders were divided into townships. By the early 1800s, the population in the surrounding townships exceeded that of the city. Eventually, mostly for police protection, the townships of Philadelphia County agreed to consolidate with the City of Philadelphia. Thus, in 1854, Philadelphia County and the City of Philadelphia became one geographic and political entity. Former townships were divided into wards with "Bristol Township" disappearing and becoming known as Ward 22. Today, that area is commonly known as Oak Lane. The designation of what was the community of Milestown disappeared from maps about 1900.

The Bristol Township that is located in Bucks County was incorporated in 1692 as Buckingham Township. The town's name was changed to Bristol in 1702 and remains to this day, a thriving municipality in the Commonwealth of Pennsylvania.

Thus, when Cantwell was researching and writing his biography of Wilson, the only Bristol Township that would have appeared on modern maps would have been the Bucks County town. The Philadelphia County township of the same name had vanished into the recesses of history.

Knowing where the Milestown School was located, which was within the confines of Philadelphia County, will hardly alter the remarkable story of Alexander Wilson's rise from being a poet, a weaver, a peddler, and a school teacher to become the universally recognized "Father of American Ornithology." Yet, for students of history there is a lesson to be learned, to wit, view historical "facts" *cum grano salis*.

LITERATURE CITED

Account Book of the Trustees of the Milestown School (Philadelphia, Pa). Records 1797–1884. Historical Society of Pennsylvania, Philadelphia, Pennsylvania. Collection Am. 248.

Burtt, E. H., Jr. and W. E. Davis Jr. 2013. Alexander Wilson: The Scot who founded American ornithology. Harvard University Press, Cambridge, Massachusetts, USA.

Cantwell, R. 1961. Alexander Wilson: naturalist and pioneer, a biography. J.B. Lippincott Company, Philadelphia, Pennsylvania, USA.

Debrandt, D. 2013 My Oak Lane Ave. www.myoaklane philadelphia.com (accessed 20 Sep 2013).

Ellwood Public School Diamond Jubilee Booklet. 1950. Ellwood Public School, Philadelphia Pennsylvania, unpublished, from the private collection of Robert Cohen, Flourtown, PA, USA.

Grosart, A. B. 1876. The poems and literary prose of Alexander Wilson, the American ornithologist. Volume 1. Alexander Gardner, Paisley, Scotland.

Hills, J. 1808. Plan of the city of Philadelphia and environs. Historical Society of Pennsylvania, Philadelphia, Pennsylvania, USA. APSdigobj3534.

Hunter, C. 1983. The life and letters of Alexander Wilson. American Philosophical Society, Philadelphia Pennsylvania, USA.

Mears, A. de B. 1890. The Old York Road: and its early associations of history and biography. 1670–1870, Harper and Brother, Philadelphia, Pennsylvania, USA.

United States Census, Bristol, Philadelphia, Pennsylvania. Series: M637; Roll: 9; Page: 291; Image: 562; Family History Library Film: 0568149.

United States Census. Bristol, Philadelphia, Pennsylvania. Roll: 42; Pages: 146–147; Image: 215; Family History Library Film: 363345.

The Wilson Journal of Ornithology 126(2):406–412, 2014

Ornithological Literature

John Faaborg, Book Review Editor

THE AVIAN MIGRANT – THE BIOLOGY OF BIRD MIGRATION. By John H. Rappole. Columbia University Press, New York, USA. 2013: xvii + 435 pages. ISBN: 978-0-231-14678-4. $80.00 (hardcover).—John H. Rappole's *The Avian Migrant* is an extensive overview of avian migration presented in 315 pages of text. Rappole distinguishes the avian migrant from resident species through an investigation of the structure of the migrant's annual cycle. Over 11 chapters, he explores topics that include the obvious annual cycle of breeding, post-breeding, fall transient period, wintering, and the spring transient period, with additional chapters on population ecology, biogeography, pathogen movement, and conservation. Rappole presents a fairly comprehensive summary of the research regarding avian migration, made evident by the more than 1,300 references cited; however, Rappole acknowledges that his text may not focus on areas that might be considered important by some.

Rappole discusses many theories regarding the evolution and development of migration in birds, and he presents differing perspectives and arguments surrounding these theories. Two appendices, written by Alan Pine, appear to give an in-depth look at the population dynamics models Rappole presents in the main body of the text. Moreover, Rappole's use of relevant case studies and notable examples throughout the text illustrates the points of his discussions. His organization of chapters based on the different periods of the annual cycle guides the reader through the life of a migrant, starting with the breeding period, and then brings the discussion full circle by ending with the spring transient period. However, much of the information presented in the subsequent chapters (e.g., biogeography) is redundant or out of place and would have been better if incorporated into the earlier chapters focused on migration. The amount of information in this book is impressive, yet there are several instances where Rappole's discussions were brief and left these readers wanting something more.

An additional concern throughout the book is the lack of current references. Most references are from the 1990s or earlier, despite the abundance of more recent research by several authors who are rarely cited in this book. As a result, the references are not representative of the present state of knowledge on avian migrants. In addition, Rappole cites himself and his students far more than any other authors, even though numerous other studies are available. Moreover, he is often highly critical of work other than his own and regularly is dismissive of avian migration research done by others. Occasionally, Rappole acknowledges that some theories he presents are "not supported by any data of which [he was] aware" (p. 45). He frames his book on several key theories about evolutionary time and the beginnings of migration, but leaves the readers without many citations or strong explanations to solidify those theories. More than once in his discussions, Rappole suggests that conservation is not science, which is a statement with which we as readers and scientists disagree.

Rappole's book includes many tables and figures, and although some are informative and useful to researchers, most are not satisfying. Figures are often larger than necessary, and many are range maps that could be found easily by interested readers from a variety of sources. Other figures, like one depicting the sexual dimorphism in resident and migratory birds, do not appropriately illustrate his point because the book was printed in grayscale. Rappole frequently uses tables to cite results from multiple studies, but he lacks summarizing statements in the text that make the tables relevant and supportive of his arguments. For example, he includes one 10 page long table in the Postbreeding Period chapter about differences in breeding and postbreeding habitat use, but this is discussed in only one sentence of text. Additionally, many tables include large text blocks with several sentences; most authors would include that information in well-organized writing and reserve tables for quick reviews of main ideas or supporting data. Also, many of his examples in tables and text were largely focused on eastern North American birds and European birds, with few examples from the western United States.

Even though the overall organization of the book is quite fitting with the annual cycle theme,

there is a lack of transition between each chapter and even between different sections within chapters. After reading a wealth of information in a given chapter, there is no summary or final conclusion(s) provided. With such an abrupt stop, the reader is left with no firm grasp of the many concepts and ideas presented. This disconnect between chapters is further strengthened by the lack of a clear introduction for subsequent chapters. Instead of providing a concise introductory paragraph to outline the ideas to be presented, Rappole forces the reader to dive headlong into a new stage of the annual cycle with little contextual material. The concluding chapter simply summarizes each individual chapter, but we feel these summaries should have been included with each corresponding chapter. Although titled "Conclusion," a more appropriate title for the last chapter would simply be "Chapter Summary" as Rappole gives no final conclusive argument. This final chapter should have focused on the overall importance of understanding the complexities of avian migrants and how these complexities apply to the scientific community; instead it offered chapter summaries and an anecdote from the past.

As graduate and undergraduate students, we feel *The Avian Migrant* would be equally suited to an undergraduate seeking supplemental reading to their main ornithology textbook or higher level academics seeking to explore Rappole's novel theories on the origin of avian migration. *The Avian Migrant* is not recommended for casual reading by birders, but should be included in research libraries.—EVAN HILL, ALESHIA FREMGEN, KIMBERLY COLE, MELISSA ROACH, and CHLOE GOODSON, Department of Fisheries and Wildlife Sciences, University of Missouri-Columbia, 302 Anheuser Busch Natural Resources Building, Columbia, MO 65211-7400, USA; e-mail: ebhgf8@mail.missouri.edu

THE MAN WHO SAVED THE WHOOPING CRANE. By Kathleen Kaska. University Press of Florida, Gainesville, Florida, USA. 2012: xii + 234 pages. ISBN: 978-0-8130-4024-0. $26.95 (hardcover).—When Robert Porter Allen was born in 1905, the U.S. population of Whooping Cranes was hovering in the low double digits. By the time of his death in 1963, the birds still numbered fewer than 100 individuals. But it is the wealth of knowledge Allen accumulated in that span—where the cranes lived, what they ate, which paths they took to migrate, how they mated and raised their young—that have allowed the population to soar to nearly 600 birds today, according to the International Crane Foundation.

That the Whooping Crane survives at all is a testament to the years of intensive, painstaking work and the undeniable passion Allen devoted to their cause. *The Man Who Saved the Whooping Cranes* documents both the scope and the fine points of his effort, which entailed heartbreak as well as unmitigated joy. Allen's biography is also the story of the rebound of a nearly extinct species, and of the evolution of wildlife conservation in the United States.

Bob Allen, as he was known, didn't start out studying Whooping Cranes. As a young boy growing up in Pennsylvania, he honed his birding skills with the usual local suspects. After two years in college and four-year stint in the Merchant Marine, he landed in New York City, talked his way into a desk job at the National Association of Audubon Societies (the progenitor of today's Audubon Society), and at 29 became sanctuaries director (with an office right next door to Roger Tory Peterson's). His first extended sojourn in the field was as leader of a project to study the threatened Roseate Spoonbill population in the Florida Keys.

It was Allen's devotion to spoonbills, and later flamingos, which prepared him to one day lead the charge to save the Whooping Cranes. He braved hurricanes; punishing heat and humidity; unreliable equipment and transportation; and predators of the insect, mammal, and reptile varieties. His intuitive sense for not only how the birds lived, but also how humans thought of and treated them, enabled him to devise recommendations for preserving the species and reducing environmental and manmade threats to its overall survival.

With his finely honed skills, a wellspring of knowledge, and an ability to convince even the surliest opponents of conservation to care about the birds' well-being, Allen stood out as the ideal choice for restoring the Whooping Crane from near-certain eradication. His work took him first to the Gulf Coast of Texas, where the dwindling population wintered in what eventually became the Aransas National Wildlife Refuge. There, with the help of wildlife officials, concerned locals, and sometimes his children, Allen conducted extensive studies of the birds' every movement.

He watched them feed, protect their territories, engage in mating dances, and raise their families.

But the Whooping Cranes only lived in Texas during the colder months. Nobody knew where migration took them, or where their nests could be found. With breeding the key to saving the species, which had dwindled to just 15 birds in 1942, Allen set out to follow them. The journeys by aircraft, canoe, and bushwhacking were arduous, and Allen suffered a good deal of privation that went far beyond a lack of creature comforts: loneliness for his family, frustration at every missed opportunity, and the pain of what was later diagnosed as a form of arthritis. Finally, after years of fruitless searching (and occasionally wrangling with U.S. and Canadian officials), Allen and his colleagues located the whoopers' summer home, in the forsaken wilds of northern Canada.

With the birds' dual homes and their migration pathways identified, preservation efforts were able to establish a foothold. Public education campaigns garnered widespread support for Whooping Cranes and reduced the amount lost to hunters. Advocates shored up protection for the whoopers' wintering and nesting grounds. Captive breeding led to the creation of an eastern population, which follows humans in ultralights between sites in Wisconsin and Florida through a program known as Operation Migration. Though Allen opposed using captive breeding methods to boost the whoopers' numbers (he preferred making every attempt to save those still living in the wild), he would likely be cheered to see this program's success.

The author paints Allen as a passionate activist, an insatiably curious scientist whose on-the-job learning made up for his lack of academic credentials, and a gifted author of works such as *The Flame Birds* and *On the Trail of Vanishing Birds*. He comes across as a creative thinker who prevailed over every obstacle to the survival of the birds, whether that meant fording literal logjams in a Canadian no-mans-land or persuading hungry citizens in Cuba and the Dominican Republic not to plunder diminishing stocks of Roseate Spoonbills and flamingos for food. Allen is also presented as a loving family man—father, husband, and brother—and an outdoorsman who relished time spent in the field.

In this respect, the book is sure to elicit nods from ornithologists who intimately know these challenges and joys themselves. They will also appreciate the lengths Allen went to in order to study his birds, and the care with which observations were recorded. The author had a plethora of material from which to draw, including field notes, reports, Allen's own journals (which feature his sketches of people and places he encountered during his travels), and his authoritative monographs which share so many rich details about the inner lives of spoonbills, flamingos, and Whooping Cranes. This is to say nothing of the personal interviews conducted with people who knew Allen, and of the documentation left behind by his former colleagues.

This largesse is, by turns, a both a blessing and a curse. In many instances, the author delves into the research to retrieve a colorful story, pithy quote, or intriguing insight. Other sections of the book, particularly the hunts in Canada for the cranes' nesting sites, are stretched out with day-by-day (or even hour-by-hour) accounts of Allen's activities. While this approach does give the reader a good sense of the tedium that no doubt marked such a monumental task, it also makes these portions of the book somewhat dense. Perhaps streamlining these sections, or providing a timeline against which to plot them, would make the reading easier going.

The book would also be enhanced with more visuals. It does include some snapshots of Allen in the field, a few of his sketches, and a rough map depicting the whoopers' migratory route and possible nest sites (before the latter were discovered). A more extensive map with the areas Allen searched in the Canadian wilderness clearly labeled would give better context to the nest-hunting accounts. Further, a map of the Florida Keys and the Caribbean would have fully illuminated his work there.

These deficits, however, do not detract from the book as a whole. It stands as a fascinating behind-the-scenes look not only at Allen's life and work, but also a love letter to Whooping Cranes and other endangered birds, as well as a tribute to the Audubon Society and the conservation movement of the 20th century. The book ends on a hopeful note, with year-by-year summaries of the "classes" of cranes that have been trained to adopt the new eastern flyway.

Still facing multiple urgent threats, the Whooping Crane is not by any means out of the figurative woods. However, due to the enormous and solid groundwork laid by Allen, the bird appears to have a fighting shot at recovery. With luck, this book will someday be a curiosity for those in the

future who have never known a time in which Whooping Cranes were in danger of disappearing together.—MEREDITH MANN, 246 West Upsal Street #C-204, Philadelphia, PA 19119, USA; e-mail: wordsbymeredith@mac.com

WALKING ON WILD SHORES: PORTRAITS OF THE NATURAL WORLD. By Kevin Winker. Two Harbors Press, Minneapolis, Minnesota, USA. 2013: ix + 353 pages. ISBN: 978-1-62652-062-2. $16.95 (paperback).—Alaska is without a doubt the greatest wilderness in the United States. Combine the majesty of this great state along with fieldwork in Central America, Bali and Russia and you have the basis for this engaging book about the exploits of Kevin Winker, roaming both tundra and tropical forests while studying birds as Curator of Birds at the University of Alaska's Museum of the North in Fairbanks, Alaska.

Winker has brought together a set of essays he has written through the years that illustrate adventure most of us can only dream about. For Alaska, not only does he describe in wonderful detail the logistics of getting to and staying on Attu and other Alaskan outposts, but he returns home to moose and the northern lights in his Fairbanks backyard. In between there is a little fishing.

In Latin America, he goes on long bus trips to reach the forests of Oaxaca and Chiapas where he and colleagues have studied wintering North American migrants. He captures well the discombobulating transition on trips to and from the darkness of an Alaskan winter into the heat and humidity of Central America.

This book is a travel log, but it is also a detailed accounting of a researcher doing work he loves. Winker's style is understated, capturing the very essence of the patience that is necessary to deal with the elements (and the inevitable bureaucracy) both near the Arctic Circle and south of the Tropic of Cancer. The result is a work, covering the breeding ranges of Artic Terns, Surfbirds, Long-tailed Jaegers, Ptarmigan and giant Pacific Wrens, that will be of interest to professional ornithologists and people just interested in nature. Along the way you can learn what an "Oosik" is and how it is used by local fishermen (do not just Google it). This is just one of many little gems Winker has sprinkled throughout the chapters. Winker's narrative will make you want to plan that trip you have always talked about so that you really experience Alaska, it's wonderful birds, mammals, rivers and mountains, and with a little luck you may run into Bob Dickerman!—JOHN M. BATES, Science and Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605-2496, USA; e-mail: jbates@fieldmuseum.org

RARE BIRDS: THE EXTRAORDINARY TALE OF THE BERMUDA PETREL AND THE MAN WHO BROUGHT IT BACK FROM EXTINCTION. By Elizabeth Gehrman. Beacon Press, Boston, Massachusetts, USA. 2012: ccxl + 240 pages, Bermuda map, Flying petrel photo. ISBN: 978-0-80-70-1076-1. $26.95 (Hardcover.).—This inspiring story of David Wingate bringing the Bermuda Petrel (known also as cahow) back from presumed extinction is one of devotion and sacrifice. It was thought that cahows had vanished because they were eaten into extinction. In the early 1900s, there was a slight chance there may still have been some birds left. The existence of the birds began to be a reality when in the early 1950s, an ornithologist and a local naturalist decided to explore whether there could still be Bermuda Petrels. A very small island in the middle of the North Atlantic was once the breeding ground for millions of Bermuda Petrels, birds that fly almost nonstop most of their lives, sleeping on the wing. David Wingate was invited to go along when the birds were rediscovered in a rocky cliff. Wingate was captivated by this discovery and became dedicated to making sure the cahow was not doomed to extinction.

Elizabeth Gehrman takes the reader through a series of historical events (not always in historical order) that includes stories of the first settlers three centuries ago. She does a good job of weaving the challenges of the work of bird conservation into this very real story. Wingate devoted much of his life and career to aide in the cahows long struggle for survival. Gehrman is able to articulate the reality of dealing with invasive species, lack of funds, political and personal barriers and the perseverance needed to succeed as she tells of Wingate's dream and obsession. While she zigzags back and forth through the story, recalled through conversations with Wingate and others, it is well told and she captures the essence of his tireless and personal dedication as well as his personal tragedies and

triumphs. This story is an inspiring story of the resilience of nature and of one human who worked so hard to save one bird species from extinction.

This is a book worth reading especially if you work in the field or know someone who works in the world of bird conservation or ornithology. The story of Wingate will inspire and resonate with bird researchers and bird lovers alike.—ALICIA F. KING, U.S. Fish and Wildlife Service, Migratory Bird Program, 4501 N. Fairfax Drive, Arlington, VA 22203, USA; e-mail: Alicia_f_king@fws.gov

SECOND ATLAS OF BREEDING BIRDS IN PENNSYLVANIA. By Andrew W. Wilson, Daniel W. Brauning, and Robert S. Mulvihill. The Pennsylvania State University Press, University Park, Pennsylvania, USA. 2012: xxiv + 592 pages. ISBN: 978-0-271-05630-2. $64.95 (hardcover).—The 2012 publication of the *Second Atlas of Breeding Birds in Pennsylvania* (hereafter *Second Atlas*) continues the legacy of Pennsylvania's bird enthusiasts of the 18th and 19th centuries, who certainly would be very proud of their 20th and 21st century colleagues. One can only imagine an 1812 gathering in Pennsylvania with 73 year-old William Bartram and 48 year-old Alexander Wilson discussing next steps for the beginnings of North American Ornithology with 20 year-old John James Audubon, Thomas Nuttall and Thomas Say. *Second Atlas* is a premier realization of skillfully-selected next steps for designing, organizing, conducting and publishing the findings of a breeding bird atlas project. *Second Atlas* should be required reading for future atlases.

The *Second Atlas* team availed itself of new technologies and the advanced skills of both modern ornithologists and citizen birders. The *Second Atlas* holds a high value to science, and its publication illustrates the efficacy of carefully choosing partners and providing field surveyors with information about survey sites in advance. Using Geographical Information Systems (GIS), land-cover images, knowledge about habitat features and their bird associates, and predictive modeling techniques, field crews surveyed the state with the knowledge of potential species within survey sites and a map of potential habitats to search. Survey teams relied on Geographical Positioning Systems (GPS) and online data entry to document *all* bird observations, not just those with the highest behavioral status observations as in many previous breeding bird atlas efforts.

Pennsylvania landscapes and natural communities were area-searched. Special crews conducted point counts to facilitate determining relative abundance and provide density data in great detail across the state. Gap analysis based on land cover data for each survey block helped surveyors locate remote areas or patchily-distributed habitats for hard-to-find species. The blocks surveyed were the same as those used in the initial *Atlas of Breeding Birds of Pennsylvania* (D. W. Brauning 1992. University of Pittsburgh Press, Pittsburgh, Pennsylvania) allowing for comparison between the two efforts.

In this new edition, editors Wilson, Brauning and Mulvihill integrated the skills and knowledge of Pennsylvania birders, world-class competitive birding teams, and research ornithologists. They organized an indispensible partnership of state and federal agencies, academia, Audubon chapters, foundations, museums, and individual citizens to provide the basic materials for education, communication and outreach.

The *Second Atlas* provides a graphical presentation of habitat association and a table of breeding phenology for many species. Atlas data for 190 species that breed in Pennsylvania are presented with two pages allotted for each species account; these include up to three maps and two tables. Each account includes a photograph of the species and a written essay on the verso that analyzes and summarizes species-specific information presented in the maps and tables. The graphic and tabular information is presented on the recto. Species accounts comprise about 60 percent of the *Second Atlas*. Fifty-two authors worked on the species accounts, which are well-written and useful to birders and scientists alike. Three maps are included with the exception of the few bird species not observed during the first atlas. The maps cover distribution during the *Second Atlas* period, distributional change between the first and second atlases, and density. The distribution maps use varying symbology to represent the category of breeding evidence codes observed during the surveys; the categories range from smallest to largest dots: possible, probable, and confirmed. The distribution change map uses colored-squares symbology to represent the distribution of birds documented on the first atlas in yellow, the *Second Atlas* in blue, and both atlases in green. Distribution dots overlay a terrain map for the state of Pennsylvania. The density map employs a six-step color gradient with the darkest

color for the highest density of singing males. There is a summary chart of species presence in atlas blocks by category for both atlases and a column for percent change. The last chart is of the U.S. Geologic Survey Breeding Bird Atlas Trends for the account species for the period of 1965–2010.

An exquisite painting by Julie Zicafoose on the cover jacket recognizes one of Pennsylvania's ornithological scholars. In remembrance of the late Dr. Kenneth C. Parkes, Curator of Birds at the Carnegie Museum of Natural History for more than 33 years, the cover depicts a female Golden-winged Warbler on a nest with her mate, a Brewster's hybrid, bringing food to her. Dr. Parkes described the blue-winged/golden-winged hybrid complex in a paper that was published in the *Wilson Bulletin* in 1951.

The *Second Atlas* provides a great template for future atlas projects. Using available technologies, building partnerships for needed skill sets, and eloquently combining the knowledge, skills, and tools into a comprehensive coverage of Pennsylvania bird distributional data, nesting phenology, relative abundances by habitat types and detailed densities for singing males statewide must be most gratifying to the editors and the 2,000 or more participants.

The *Second Atlas* is a valuable tool for Pennsylvania bird study for professional ornithologists, seasoned birders, and conservation-minded nature enthusiasts. Anyone planning to design a bird atlas project for their state should study this masterful and successful example. Any birder visiting Pennsylvania should be sure to have a copy of this book at home or in the car. This is a nice addition to any bird library because of the breadth of natural history information included.—BRAD JACOBS, Wildlife Division, Missouri Department of Conservation, P. O. Box 180, Jefferson City, MO 65102-0180, USA; e-mail: brad.jacobs@mdc.mo.gov

CUCKOOS OF THE WORLD. By Johannes Erritzøe, Clive F. Mann, Frederik P. Brammer, and Richard A. Fuller. Helm Identification Guides, Christopher Helm, London, UK. 2012: 544 pages. ISBN: 978-0-71366-034-0. $110.00 (hardcover).—From the perspective of cuckoo diversity, North America is sadly impoverished. True, we have the Yellow-billed and Black-billed cuckoos (*Coccyzus americanus* and *C. erythropthalmus*), with their slow, peering habits and resonant voices. In the Gulf Coast or the Southwest one might catch a glimpse of the occasional ani or roadrunner. But to experience the full richness of this ancient family – the koels, malkohas, coucals, drongo-cuckoos, hawk-cuckoos, and bronze-cuckoos; the ground cuckoos of the Amazon; the cobalt-colored couas of Madagascar – we have to venture farther afield. Fortunately, we now have *Cuckoos of the World*, the latest volume in the newly revamped series of Helm Identification Guides, to give us the tour.

This beautifully produced guide uses both photographs and color plates to illustrate all 144 cuckoo species of the world. It consists of three sections: an introduction with brief essays on cuckoo morphology, systematics, and general information; 36 color plates depicting each species; and individual species accounts, which take up most of the volume. Like the other recent volumes in the series, it is a hybrid between a traditional field guide and a family-level monograph, providing comprehensive information on breeding biology, natural history, and conservation.

Visually, *Cuckoos of the World* is stunning. The color plates, painted by Richard Allen, Jan Wilczur, Martin Woodcock, and Tim Warfolk, are extremely good, even though variations in style are occasionally noticeable. The artists have done a wonderful job of capturing the characteristic postures of different species as well as the plumage details – the roadrunners, in particular, seem ready to skitter right off the page. Most species are represented by several plumages for different ages and subspecies, ranging from a single illustration for the extinct Snail Coua (*Coua delandei*) to 13 for the highly variable Common Koel (*Eudynamys scolopaceus*). The only disappointing aspect of the plates is the odd scaling: the New World species, including the magnificent ground cuckoos, are reproduced at a disproportionately small size, whereas the Palearctic *Cuculus* species are gargantuan by comparison.

The photographs that accompany almost every species account are equally outstanding, and add tremendously to the value and attractiveness of the book. Nearly all of the photographs were taken in the field and show the species in its characteristic habitat, providing context and immediacy. Several photos depict fledglings of the brood-parasitic species being fed by their unwitting hosts. Others capture behaviors like sunning, displaying, or foraging (one of my favorites is of a Madagascar Coucal (*Centropus toulou*) attacking an upside-down, goggle-eyed chameleon). The range maps are large and easy to read, with dotted lines usefully

indicating the distributions of subspecies. (The maps, as well as the individual records on which they are based, are available at http://www.fullerlab.org/cuckoos/).

Although the range maps are generally well done, it is often necessary to read the text to get a sense of whether an area is actually part of a species' distribution or merely represented by a handful of vagrancy records. North American birders will notice, for instance, that the wintering range of Groove-billed Ani (*Crotophaga sulcirostris*) is shown as extending over the entire Gulf Coast and most of Florida – an area where it is quite rare. In other cases it is difficult to tell whether a patchy distribution appears that way because of biogeography – as a result of naturally isolated habitat patches, for example – or because of missing data.

Each species account is several pages long and is divided into sections on taxonomy, field identification, voice, description, biometrics, molt, distribution, habitat, behavior, breeding, diet, and conservation status. Unfortunately, the text suffers in comparison with the vivid photographs and paintings. The accounts are thorough and well-researched, but the writing is so highly compressed as to be occasionally unreadable. Long lists of citations are placed at the end of each paragraph, making it impossible to tell which reference pertains to which piece of information. In addition, much of the information in the species accounts has already been well covered in Payne's monograph, *The Cuckoos* (R. Payne, 2005, Oxford University Press). The descriptions of habitat and voice, for example, are generally quite similar, and the measurements in the biometrics sections appear to have been copied almost verbatim. Some of this is inevitable, given that relatively little time elapsed between the publication of the two books, but I was disappointed that the authors missed several opportunities to discuss interesting aspects of cuckoo biology that were not covered by Payne. For example, although the authors discuss the brood-parasitic habits of the Eurasian cuckoos at great length, they fail to mention the uncanny resemblance between the Oriental drongo-cuckoos (*Surniculus*) and the unrelated drongos (*Dicrurus*), a fascinating case of mimicry that is probably also an adaptation to brood parasitism. Similarly, the introductory essay on breeding behavior focuses entirely on the Eurasian brood-parasitic cuckoos, scarcely even mentioning the polyandrous coucals, the facultatively parasitic *Coccyzus* cuckoos, or the bizarre communal breeding systems of the crotophagine cuckoos (*Crotophaga* and *Guira*). The introductory material overall is rather brief, and readers interested in serious treatments of cuckoo evolution and behavior will find that this book is no substitute for Payne (2005).

On the whole, however, these omissions are understandable, given the visual focus of the book and the vast amount of information that it summarizes. The quality of the color plates and the photographs alone are enough to justify the cost of the volume. Like most "identification guides" of global scope, it is not intended to be used in the field, but any birder or scientist interested in cuckoos will find it to be a beautiful and invaluable reference.—CHRISTINA RIEHL, Museum of Comparative Zoology, Harvard University, 24 Oxford Street, Cambridge, MA 02138, USA; e-mail: criehl@fas.harvard.edu

The Wilson Journal of Ornithology 126(2):413, 2014

EDUCATION OF A YOUNG POET AND FUTURE ORNITHOLOGIST

Philadelphia was the birthplace of American Ornithology. Alexander Wilson was the father. Like so many of America's forefathers, he was an immigrant. He was born in Paisley, Scotland. His parents were Alexander Wilson, known as Saunders, a former soldier and a weaver by trade, the latter requiring skill and artistic judgment, and Mary McNab, beautiful and talented. Sandy was an only son with two older sisters. His mother intended that he become a Presbyterian minister, a learned and respected profession in eighteenth century Scotland. To that end he was enrolled in Paisley Grammar School and privately tutored by Mr. Barlas, a divinity student. The elegant language and imagery of *American Ornithology* may derive from the time he spent reading the bible with Mr. Barlas who undoubtedly chose the King James translation commissioned by the first Scot to ascend the throne of a united Scotland, Ireland and England. However, when Sandy was not quite ten, his mother died. His father married a widow with two children. A sixth child was soon added to the family. Money was tight so Sandy left school to work as a cowherd for Mr. Stevenson of Threepwood. At the time, Scotland had few fences, walls, or hedgerows, so a herd boy was necessary to keep livestock on designated grazing land. Young Sandy spent long solitary days walking the nearby hills tending cows. When his charges slowed to graze or settled down to ruminate, he watched birds or lay in the grass and invented verses. He probably recited these to his cud-chewing charges. Speculation aside, the first of six stanzas of a ballad written in 1778 or 1779, shows the boy's considerable command of language and rhythm:

> Castle Semple stands sae sweet,
> The parks around are bonnie, O;
> The ewes and lambs ye'll hear them bleat,
> And the herd's name is Johnnie, O

Edward H. Burtt, Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH 43015

THE WILSON JOURNAL OF ORNITHOLOGY

Editor MARY BOMBERGER BROWN
School of Natural Resources
University of Nebraska
3310 Holdrege Street
Lincoln, NE 68583-0995
E-mail: wjo@unl.edu

Associate Editor MELISSA J. PANELLA

Editorial Board RICHARD C. BANKS
JACK CLINTON EITNIEAR
T.J. FONTAINE
SCOTT W. GILLIHAN
REBECCA J. SAFRAN

Review Editor JOHN FAABORG
Division of Biological Sciences
University of Missouri-Columbia
110 Tucker Hall
Columbia, MO 65211-7400
E-mail: FaaborgJ@missouri.edu

GUIDELINES FOR AUTHORS

Please consult the detailed "Guidelines for Authors" found on the Wilson Ornithological Society web site (http://www.wilsonsociety.org) or the Wilson Journal of Ornithology web site (http://wjoonline.org). All manuscript submissions should be sent to Mary Bomberger Brown, Editor, *The Wilson Journal of Ornithology* via e-mail at wjo@unl.edu or surface mail at School of Natural Resources, University of Nebraska, 3310 Holdrege Street, Lincoln, NE 68583-0995.

NOTICE OF CHANGE OF ADDRESS

Notify the Society immediately if your address changes. Send your complete new address to Ornithological Societies of North America, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

The permanent mailing address of the Wilson Ornithological Society is: %The Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109, USA. Persons having business with any of the officers may address them at their various addresses given on the inside of the front cover, and all matters pertaining to the journal should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Lindsay A. Walters, Department of Biological Sciences, Northern Kentucky University, Highland Heights, KY 41099; e-mail: waltersl3@nku.edu

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution. The fund is administered by the Library Committee. Jerome A. Jackson, Florida Gulf Coast Univeristy, is Chairman of the Committee. The Library currently receives over 200 periodicals as gifts and in exchange for *The Wilson Journal of Ornithology*. For information on the Library and our holdings, see the Society's web page at http://www.wilsonsociety.org. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: Josselyn Van Tyne Memorial Library, Museum of Zoology, The University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA. Contributions to the New Book Fund should be sent to the Treasurer.

This issue of *The Wilson Journal of Ornithology* was published on 11 July 2014.

Continued from outside back cover

321 Distribution of color-morphs of the Eastern Screech-Owl in Iowa
Tex A. Sordahl

Short Communications

333 Snow Buntings sing individually distinctive songs and show inter-annual variation in song structure
Sarah Baldo, Daniel J. Mennill, Sarah Guindre-Parker, H. Grant Gilchrist, and Oliver P. Love

338 Hybridization of a Lesser Black-backed Gull and Herring Gulls in eastern North America
Julie C. Ellis, Steven M. Bogdanowicz, Mary Caswell Stoddard, and L. William Clark

345 Testing for behavioral lateralization in observational data: a Monte Carlo approach applied to neck-looping in American Flamingos
Austin L. Hughes, Jonathan Cauthen, and Caroline Driscoll

352 Dispersal patterns suggest two breeding populations of Piping Plovers in eastern Canada
Diane L. Amirault-Langlais, Tara L. Imlay, and Andrew W. Boyne

359 Modeling Greater Roadrunners' (*Geococcyx californianus*) habitat use in west Texas
Andrea E. Montalvo, Dean Ransom, Jr., and Roel R. Lopez

366 Light pollution allows the Northern Mockingbird (*Mimus polyglottos*) to feed nestlings after dark
Christine M. Stracey, Brady Wynn, and Scott K. Robinson

370 Provisioning behavior of male and female Indigo Buntings
Gary Ritchison and Kimberly P. Little

374 Factors influencing seed species selection by wild birds at feeders
Stacey M. Johansen, David J. Horn, and Travis E. Wilcoxen

381 Nesting of Laughing Falcons (*Herpetotheres cachinnans*) in the Pantanal, Brazil, with remarks on young plumage and nestling vocalization
Karlla V. C. Barbosa, Thiago Filadelfo, Monalyssa Camandaroba, Thiago V. V. Costa, and Neiva M. R. Guedes

389 First nest record of Red-throated Caracara (*Ibycter americanus*) for Middle America
Ruth E. Bennett, Isidro Zuniga, Mark Bonta, David L. Anderson, Sean McCann, and Luis Herrera

393 Breeding biology of Squacco Herons (*Ardeola ralloides*) in northern Tunisia
Aymen Nefla, Wided Tlili, Ridha Ouni, and Saïd Nouira

401 Locating Alexander Wilson's Bristol Township and the Milestown School
Albert Filemyr and Jeff Holt

406 **Ornithological Literature**
John Faaborg, Book Review Editor

413 Education of a young poet and future ornithologist
Edward H. Burtt, Jr.

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 126, Number 2 CONTENTS June 2014

Major Articles

179 The avian biogeography of an Amazonian headwater: the Upper Ucayali River, Peru
Michael G. Harvey, Glenn F. Seeholzer, Daniel Cáceres A., Benjamin M. Winger, Jose G. Tello, Flor Hernández Camacho, Miguel A. Aponte Justiniano, Caroline D. Judy, Sheila Figueroa Ramírez, Ryan S. Terrill, Clare E. Brown, Luis Alberto Alza León, Gustavo Bravo, Mariela Combe, Omar Custodio, Alessandra Quiñonez Zumaeta, Abraham Urbay Tello, Willy Antonio Garcia Bravo, Aaron Z. Savit, Frans Willy Pezo Ruiz, William M. Mauck III, and Olivier Barden

192 150 years of changes in bird life in Cambridge, Massachusetts from 1860 to 2012
Michael W. Strohbach, Andrew Hrycyna, and Paige S. Warren

207 The historical distribution of Gunnison Sage-Grouse in Colorado
Clait E. Braun, Sara J. Oyler-McCance, Jennifer A. Nehring, Michelle L. Commons, Jessica R. Young, and Kim M. Potter

218 Phylogeography of the Gambel's Quail (*Callipepla gambelii*) of western North America
Damon Williford, Randy W. DeYoung, Rodney L. Honeycutt, Leonard A. Brennan, Fidel Hernández, James R. Heffelfinger, and Louis A. Harveson

236 Range expansion and the breakdown of Bergmann's Rule in Red-bellied Woodpeckers (*Melanerpes carolinus*)
Jeremy J. Kirchman and Kathryn J. Schneider

249 Exogenous testosterone in male Downy Woodpeckers leads to reduced calling behavior of both males and their female partners during the non-breeding period
James S. Kellam and Jeffrey R. Lucas

261 Testosterone production in non-breeding Northern Cardinals (*Cardinalis cardinalis*): is temperature influential?
Jodie M. Jawor, Jeffrey D. Hooker, and Richard Mohn

269 Singing seaside: Pacific Wrens (*Troglodytes pacificus*) change their songs in the presence of natural and anthropogenic noise
Danielle C. Gough, Daniel J. Mennill, and Erica Nol

279 Reproductive success and habitat characteristics of Golden-winged Warblers in high-elevation pasturelands
Kyle R. Aldinger and Petra Bohall Wood

288 Selection of forest canopy gaps by male Cerulean Warblers in West Virginia
Kelly A. Perkins and Petra Bohall Wood

298 Habitat requirements of the endangered Amami Thrush (*Zoothera dauma major*), endemic to Amami-Oshima Island, southwestern Japan
Taku Mizuta

305 Northern Saw-whet Owl: regional patterns for fall migration and demographics revealed by banding data
John L. Confer, L. Leann Kanda, and Ireyena Li

Continued on inside back cover